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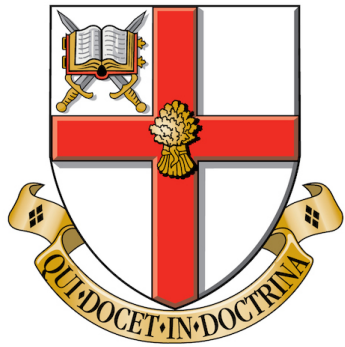
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University of Chester

Mathematical Modelling of Mutualism in Population Ecology

by

Andrew P Rowntree B.Sc(Hons)

Submitted to the School of Computer Science and Mathematics,

Faculty of Science and Engineering

in partial fulfilment of the requirements for the degree of

Master of Science in Mathematics

at the

UNIVERSITY OF CHESTER

September 2014

Author

School of Computer Science and Mathematics

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September 29, 2014

Supervised by

Dr. Jason Roberts & Dr. Nikos Kavallaris

Senior Lecturers

Declaration of Authorship

I, Andrew P Rowntree, declare that this dissertation titled, 'Mathematical Modelling of Mutualism in Population Ecology' and the work presented in it are my own. I confirm that:

- This work was undertaken completely while in candidature for a Masters of Science degree at the University of Chester.
- Where I have consulted the published work of others, this is always clearly attributed.
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Signed

ANDREW P ROWNTREE

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Abstract

This research dissertation focuses on the symbiotic interaction of mutualism, we give explanations as to what it is before mathematically modelling population dynamics of two species displaying mutualistic behaviour. Throughout the course of this dissertation, we shall be re-examining the work done in the book by Kot [16] and the paper by Joharjee and Roberts [32], whilst providing further explanations of the mathematics involved and the steps taken. We begin by constructing a model for mutualism before attempting to improve the model in order to make it more realistic. We go on to add delays to our improved model and determine the stability of its equilibrium points. We formulate models via piecewise constant arguments and via a simple Euler scheme before determining stability for both systems. A graphical comparison will then be made to explain the differences in behaviour between the two discretised systems.

Dissertation Supervisors: Dr. Jason Roberts & Dr. Nikos Kavallaris
Titles: Senior Lecturers in Mathematics

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In Memory of Tudor Endersby and Lionel 'Bill' Rowntree

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Chapter 1

Introduction

1.1 What is mutualism?

Mutualism is an interaction between different species in which they benefit each others existence.

1.2 Why are we studying mutualism?

It is said by Boucher that Elementary ecology literature tells us that organisms interact in three fundamental ways; competition, predation and mutualism [3]. There has been plenty of credible work done in the areas of predator-prey and competition models, however we find that when researching our chosen area, it has been largely neglected in ecological literature until very recently. It is hard not to agree with Bascompte and Jordano's view, that mutualism represents one of the main mechanisms for shaping animal's and plant's life histories and that understanding mutualistic interactions and their consequences in species-rich communities remains one of the most challenging tasks in ecology [1]. The importance of mutualism is surely cemented when we find that it was even noted early on by Charles Darwin on his travels; "If such great moths were to become extinct in Madagascar, assuredly the *Angraecum* would become extinct" [5], he saw with this example that certain species would have perished had they not have found mutualistic partners. So, we are studying mutualism in order to gain a better understanding of an area of ecology that in terms of research is in short supply when compared to its peers.

1.2.1 Examples of mutualism

Having thoroughly studied the natural history of mutualisms, Janzen [14] argued that most mutualisms can be classified into one of four types;

Seed-dispersal mutualism

A lot of plants rely on animals to carry their seeds to favourable destinations. Plants frequently produce fruits and nuts to attract the animals, the food also serves as positive reinforcement for the animals to return again. Squirrels are very popular dispersal agents, they will collect acorns and nuts from trees and bury them elsewhere before forgetting about them hence allowing them to grow into other trees. Other examples include birds such as the Western Scrub Jay (*Aphelocoma californica*) who use the technique of 'caching' which involves storing the food like acorns or insects in a cache for later retrieval. They

will carry seeds long distances and cache them in small clumps, where they may germinate [16].

Pollination mutualism

Pollination is the transfer of a plant's pollen grain before fertilisation. The classic example here is between bees and flowers, bees use the flowers for nectar and in return pollinate other flowers that they encounter on their travels. In gymnosperms, the transfer is from a pollen-producing cone directly to an ovule. In angiosperms, the transfer is from an anther to a stigma. Most gymnosperms are wind-pollinated. In contrast, many angiosperms are animal pollinated. The obvious advantage of animal pollination is that pollen may be transferred far from the host anther in a way that promotes outbreeding and genetic variability. Angiosperm flowers often reward pollinators with nectar and pollen to promote this process. Plant-pollinator mutualisms are particularly important, and involve nearly 170,000 plant and 200,000 animal species [19, 16].

Digestive mutualism

The guts of many animals are filled with mutualists (e.g. bacteria, yeast etc.) that help to break down food. Often, the host animal is unable to digest the food on its own. Animals such as cattle, deer and sheep rely on bacteria to break down plant cellulose into subdigestible subunits. The microorganisms are rewarded for this behaviour by having an environment in which they can survive i.e. the animal's gut [16].

Protection mutualism

Protection mutualism is when one species protects another from predators, usually for some kind of return favour. A very good example of a protection mutualism is one between clown fish and sea anemones. The clown fish are immune to the stinging nematocysts of giant sea anemones and will feed and nest amongst their tentacles. Horse mackerels appear to have a similar relationship with Portuguese man-of-war jellyfish [16].

There most likely exists many more types of mutualisms that occur throughout the natural world many of which may be undiscovered by science.

1.2.2 Dependency of the mutualism

The dependency of mutualism refers to how much a species is in need of the interaction, we shall define the notes two different types of dependency that are used by the ecologist Kot [16];

Definition 1 (Facultative Mutualism). A type of mutualism in which the interacting species derive benefit from each other but are not fully dependent that each cannot survive without the other. This is the most common type of mutualism and is exemplified by plants producing fruit that is eaten by birds and the birds helping to dispose the seeds through excretion [2].

Definition 2 (Obligate Mutualism). A type of mutualism in which the species involved are in close proximity and interdependent with one another in a way that one cannot survive without the other. A good example of this is between fungus and alga forming lichen. In nature, the fungus in lichen provides the alga with water and minerals while the

alga uses the minerals and water to make food for the fungus and itself (by photosynthesis.) When the alga and fungus of lichens were cultured separately under laboratory conditions, both of them cannot grow without the symbiotic partner [2].

In the next chapter we shall attempt to construct a mathematical model to represent mutualism.

Chapter 2

Modelling mutualism

2.1 Initial attempt at modelling mutualism

Throughout the next two chapters we will follow the work done in chapters 12 and 13 by Kot in the book ‘Elements of Mathematical Ecology’ and also reproduce the graphs found there through a MATLAB program called ‘pplane7’ [25].

Let us begin by assuming that we have two species, 1 and 2, each with population sizes N_1 and N_2 respectively that grow logistically¹ in the absence of the other. Each species has a per capita growth rate that decreases linearly with its population size. Therefore we begin with the following model

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1}{K_1} \right) \quad (2.1a)$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2}{K_2} \right), \quad (2.1b)$$

where each species has its own respective intrinsic rate of growth and its own respective carrying capacity K_1 and K_2 . Now let’s add competition to the model; we can do this by assuming the effect of interspecific competition² is similar to that of intraspecific crowding. Due to competition, each individual of the second species causes a decrease in the per capita growth of the first species, and vice versa. Now, because the two species are different, individuals from different species (heterospecific) may have a stronger effect or a weaker effect on the per capita growth rate than individuals from the same species (conspecific). To parameterise this effect, we introduce a pair of competition coefficients α_{12} and α_{21} , that measure the strength of the effect of species 2 on species 1 and of species 1 on species 2 respectively. So, we let

¹Logistic growth - Population growth in which the growth rate decreases with increasing number of individuals until it becomes zero when the population reaches a maximum[20].

²Interspecific competition is a form of competition in which individuals of different species compete for the same resource. The other form of competition is intraspecific competition, which involves organisms of the same species [12].

$$\begin{aligned}
N_1 &\rightarrow N_1 + \alpha_{12}N_2 \\
&\text{and} \\
N_2 &\rightarrow N_2 + \alpha_{21}N_1
\end{aligned}$$

then the system (2.1a) - (2.1b) becomes the Lotka-Volterra competition model

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1 \left(1 - \frac{N_1 + \alpha_{12}N_2}{K_1} \right) \quad (2.2a)$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2 \left(1 - \frac{N_2 + \alpha_{21}N_1}{K_2} \right). \quad (2.2b)$$

Let us take out a factor of $\frac{1}{K_1}$ and $\frac{1}{K_2}$ and multiply both sides by N_1 and N_2 in respective equations to arrive at a more concise model

$$\frac{dN_1}{dt} = \frac{r_1}{K_1} N_1 (K_1 - N_1 - \alpha_{12}N_2) \quad (2.3a)$$

$$\frac{dN_2}{dt} = \frac{r_2}{K_2} N_2 (K_2 - N_2 - \alpha_{21}N_1). \quad (2.3b)$$

Now, we want to modify this competition model to create a mutualism model between the two species. To do this, it seems a natural step to simply change the competition coefficients α_{12} and α_{21} from having a negative effect to a positive effect on both equations since mutualism is defined as a beneficial interaction. So, let's change their signs from $-$ to $+$, this gives us

$$\frac{dN_1}{dt} = \frac{r_1}{K_1} N_1 (K_1 - N_1 + \alpha_{12}N_2) \quad (2.4a)$$

$$\frac{dN_2}{dt} = \frac{r_2}{K_2} N_2 (K_2 - N_2 + \alpha_{21}N_1). \quad (2.4b)$$

This is now a model for facultative mutualism so far as the parameters

$$r_1 > 0, r_2 > 0, K_1 > 0 \text{ and } K_2 > 0, \quad (2.5)$$

in other words, each species can survive without its mutualist.

We note that the model would be for obligate mutualism should the parameters be set as follows

$$r_1 < 0, r_2 < 0, K_1 < 0 \text{ and } K_2 < 0. \quad (2.6)$$

2.1.1 Finding and determining stability of equilibrium points of the system (2.4a)-(2.4b)

We can find the equilibrium points of the system (2.4a) - (2.4b) by setting $\frac{dN_1}{dt} = \frac{dN_2}{dt} = 0$

So, let's consider (2.4a), we set

$$\frac{dN_1}{dt} = 0$$

i.e.

$$\frac{r_1}{K_1} N_1 (K_1 - N_1 + \alpha_{12} N_2) = 0$$

therefore, either

$$\frac{r_1}{K_1} N_1 = 0 \quad \text{or} \quad K_1 - N_1 + \alpha_{12} N_2 = 0$$

which implies that our zero-growth isoclines for N_1 are

$$N_1 = 0 \quad \text{and} \quad N_1 = K_1 + \alpha_{12} N_2$$

Similarly setting $\frac{dN_2}{dt} = 0$, we get

$$\frac{r_2}{K_2} N_2 (K_2 - N_2 + \alpha_{21} N_1) = 0$$

hence either

$$\frac{r_2}{K_2} N_2 = 0 \quad \text{or} \quad K_2 - N_2 + \alpha_{21} N_1 = 0$$

which implies that our zero-growth isoclines for N_2 are

$$N_2 = 0 \quad \text{and} \quad N_2 = K_2 + \alpha_{21} N_1.$$

So, our four equilibrium points are

$(N_1^*, N_2^*) = (0, 0)$ in which both species die out, as shown in figure 2.1.

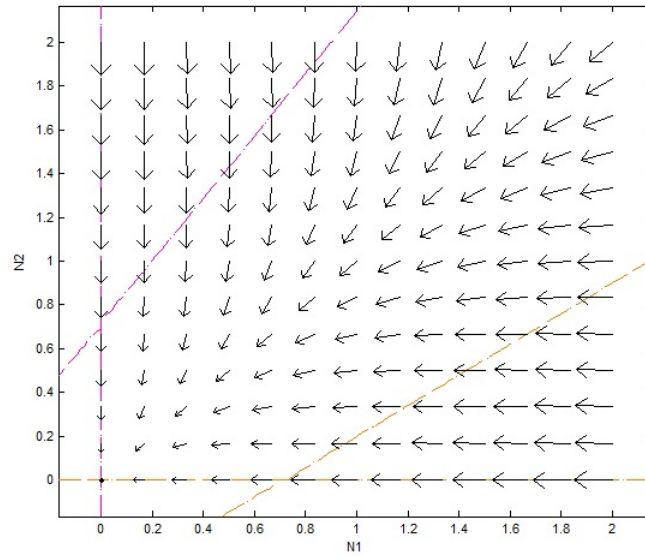


Figure 2.1: Obligate mutualism phase portrait for $\alpha_{12}\alpha_{21} < 1$.

$(N_1^*, N_2^*) = (K_1, 0)$ in which species 2 dies out and species 1 settles at its carrying capacity.

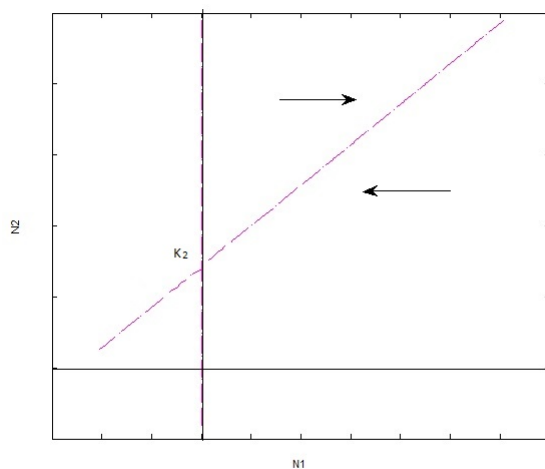


Figure 2.2: N_1 zero-growth isoclines, $K_1 < 0$.

In Figure 2.2 we see that to the left of the line $N_1 = K_1 + \alpha_{12}N_2$, N_1 increases and to the right of this line N_1 decreases.

$(N_1^*, N_2^*) = (0, K_2)$ in which species 1 dies out and species 2 settles at its carrying capacity.

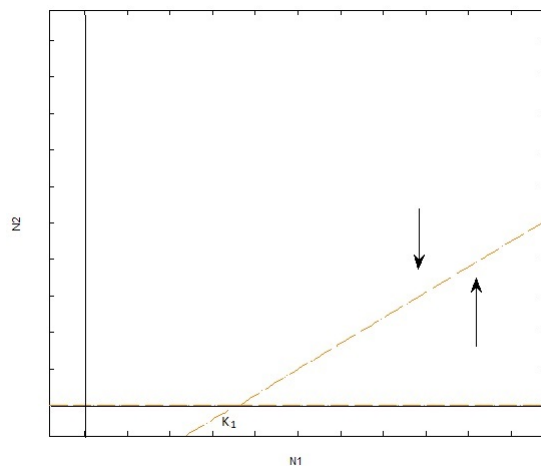


Figure 2.3: N_2 zero-growth isoclines, $K_2 < 0$.

In Figure 2.3 we see that below the line $N_2 = K_2 + \alpha_{21}N_1$, N_2 increases and above this line N_2 decreases.

$(N_1^*, N_2^*) = (K_1 + \alpha_{12}N_2^*, K_2 + \alpha_{21}N_1^*)$ which is our non-trivial equilibrium point that lies in the positive quadrant.

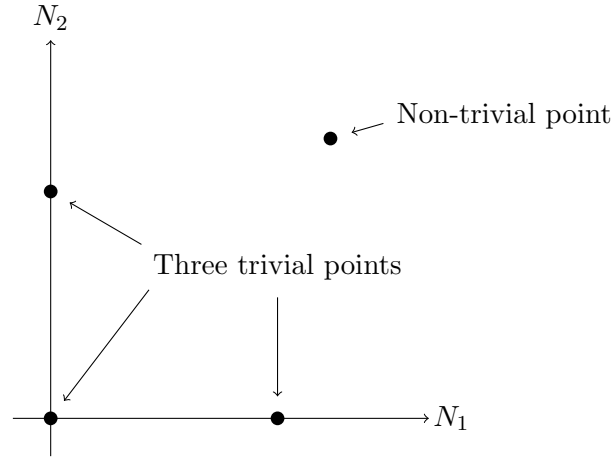
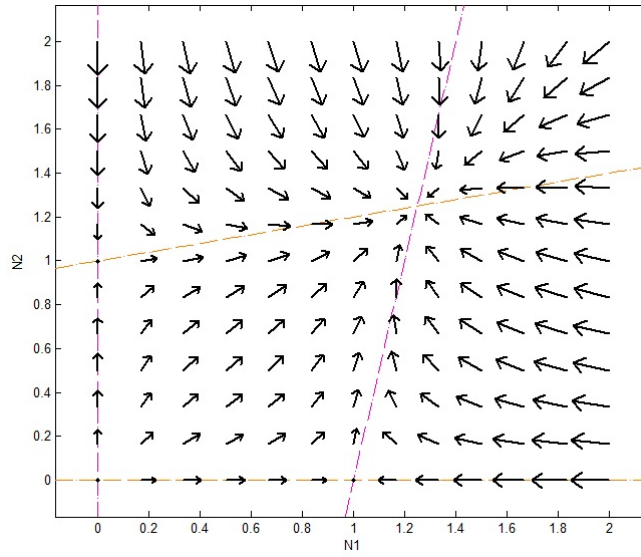


Figure 2.4: Graph showing an arbitrary (N_1, N_2) plane with its four equilibrium points.

Note that the zero-growth isoclines divide each graph into two parts. To the left and below of the isocline (in respective graphs) the population size increases because the combined abundances of both species are less than the carrying capacity of the one, while to the right and above of the isocline (in respective graphs) the population size decreases because the combined abundances are greater than the carrying capacity. For Figure 2.3, the isocline intersects the graph on the N_1 -axis when N_1 reaches its carrying capacity (K_1) and no individuals of species 2 are present. For Figure 2.2, the isocline intersects the graph on the N_2 -axis when N_2 reaches its carrying capacity (K_2) and no individuals of species 1 are present.

Figure 2.5: Facultative mutualism phase portrait for $\alpha_{12}\alpha_{21} < 1$

The zero-growth isoclines

$$N_1 = K_1 + \alpha_{12}N_2 \quad \text{and} \quad N_2 = K_2 + \alpha_{21}N_1$$

may either converge or diverge. They converge if

$$\frac{1}{\alpha_{12}} > \alpha_{21} \quad \Rightarrow \quad \alpha_{12}\alpha_{21} < 1$$

In this case, the two isoclines cross and orbits approach a stable node in the interior of the first quadrant (as shown in Figure 2.5). Since the slopes of the two zero-growth isoclines are positive, the coordinates of this equilibrium are greater than the carrying capacities K_1 and K_2 ; each species surpasses its carrying capacity because of its mutualist.

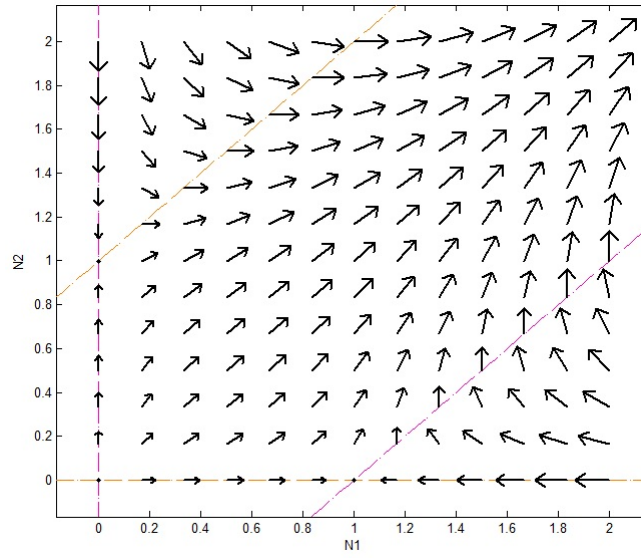
If

$$\alpha_{12}\alpha_{21} > 1$$

then the zero growth isoclines

$$N_1 = K_1 + \alpha_{12}N_2 \quad \text{and} \quad N_2 = K_2 + \alpha_{21}N_1$$

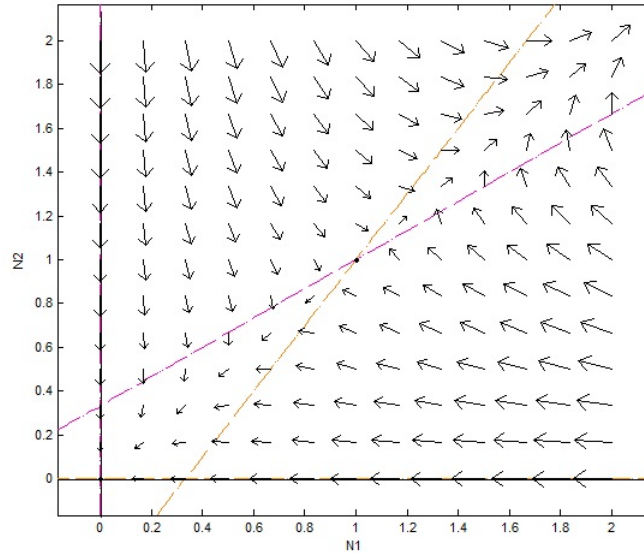
diverge. In this case, the zero-growth isoclines do not cross and the only nontrivial equilibrium point in the first quadrant exists at the point (∞, ∞) .

Figure 2.6: Facultative mutualism phase portrait for $\alpha_{12}\alpha_{21} > 1$

The populations undergo unlimited growth (as shown in Figure 2.6) this is also known as an "orgy of mutual benefaction" a phase coined by the ecologist May [26].

Again, if the interaction is strong with

$$\alpha_{12}\alpha_{21} > 1$$

Figure 2.7: Obligate mutualism phase portrait for $\alpha_{12}\alpha_{21} > 1$

then we have a saddle point. If mutualist densities are low, i.e. there are too few mutualists to rescue either population then both populations become extinct. If mutualist

densities are high, both species increase to another orgy of mutual benefaction (as shown in figure 2.7).

The orbits of our mutualism model have either tended to an equilibrium or diverged to infinity. However, we must make sure that there are no limit cycles³ that we have missed. To do this, we shall prove that the system is cooperative.

Definition 3 (Cooperative system). The system

$$\begin{aligned}\frac{dN_1}{dt} &= \phi(N_1, N_2) \\ \frac{dN_2}{dt} &= \sigma(N_1, N_2)\end{aligned}$$

defined on $D \subseteq \mathbb{R}^2$ is cooperative if

$$\frac{\partial \phi}{\partial N_2} \geq 0, \quad \frac{\partial \sigma}{\partial N_1} \geq 0 \quad (2.7)$$

for all $(N_1, N_2) \in D$.

For the model (2.4a) - (2.4b), we let

$$\begin{aligned}\frac{dN_1}{dt} &= \frac{r_1}{K_1} N_1 (K_1 - N_1 + \alpha_{12} N_2) = f_1(N_1, N_2) \\ \frac{dN_2}{dt} &= \frac{r_2}{K_2} N_2 (K_2 - N_2 + \alpha_{21} N_1) = g_1(N_1, N_2)\end{aligned}$$

so, we get

$$\begin{aligned}\frac{\partial f_1}{\partial N_2} &= \frac{\partial}{\partial N_2} \left(\frac{r_1}{K_1} N_1 (K_1 - N_1 + \alpha_{12} N_2) \right) \\ &= \alpha_{12} \frac{r_1}{K_1} N_1\end{aligned}$$

and

$$\begin{aligned}\frac{\partial g_1}{\partial N_1} &= \frac{\partial}{\partial N_1} \left(\frac{r_2}{K_2} N_2 (K_2 - N_2 + \alpha_{21} N_1) \right) \\ &= \alpha_{21} \frac{r_2}{K_2} N_2\end{aligned}$$

clearly

$$\frac{\partial f_1}{\partial N_2} \geq 0, \quad \text{and} \quad \frac{\partial g_1}{\partial N_1} \geq 0, \quad (2.8)$$

³A limit cycle is a closed trajectory in phase space having the property that at least one other trajectory spirals into it either as time approaches infinity or as time approaches negative infinity [22].

therefore our system (2.4a) - (2.4b) is cooperative on the invariant quadrant.

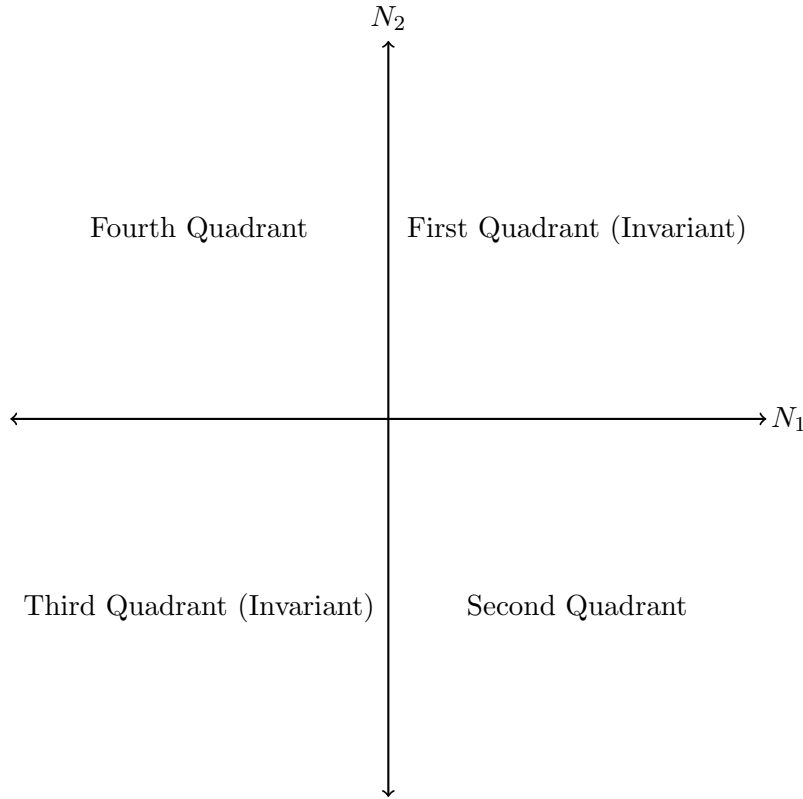


Figure 2.8: Graph illustrating the four quadrants an arbitrary (N_1, N_2) plane

We shall now state and prove theorem 2.1.

Theorem 2.1. The orbits of a cooperative system either converge to equilibria or diverge to infinity.

Proof. Every trajectory of a system generates an orbit in this (N_1, N_2) plane (see figure 2.8). If the system is cooperative everywhere, the first quadrant of the (N_1, N_2) plane is invariant. To exhibit this, consider an orbit that attempts to leave the first quadrant by crossing the positive N_2 -axis. Using our definition for cooperativity, we can show that

$$\frac{d^2 N_1}{dt^2} = \frac{\partial \phi}{\partial N_1} \frac{dN_1}{dt} + \frac{\partial \phi}{\partial N_2} \frac{dN_2}{dt} = \frac{\partial \phi}{\partial N_2} \frac{dN_2}{dt} > 0 \quad (2.9)$$

on the positive N_2 -axis. Thus, the orbit cannot cross the positive N_1 -axis. We also note that the orbit cannot pass through the origin, as this would imply that the original trajectory passes through a rest point. We can show similarly that the third quadrant is invariant. As $t \rightarrow \infty$, N_1 's and N_2 's signs will stay constant, i.e. if we start in the first or third quadrant, we stay in that quadrant. If we start in the second or fourth quadrant, we either stay there or move to one of the two invariant quadrants [16]. \square

2.2 Is this a suitable model?

This is not a suitable model for mutualism due to the fact that there exists an equilibrium point at (∞, ∞) when $\alpha_{12}\alpha_{21} > 1$ as illustrated in figures 2.6 and 2.7. This is not realistic

because we cannot have infinite populations. We have been allowing the models to grow in an unbounded manner which is also totally unrealistic since physical aspects of our world such as space limitations and availability of resources will always bound growth of populations. We also cannot entertain the idea of populations being negative in reality. With these problems identified, we shall attempt to construct mutualism models that reflect reality better as we progress through this paper.

Chapter 3

Attempts at constructing a more realistic model

We must attempt to construct a model that is more suited to a real world situation. One approach to preventing unlimited growth is to construct a resource-based model.

3.1 A Resource-Based Model

This model is taken exclusively from Kot [16]. An example can be found in the work of Lee *et al* [21] on the interaction between a lactic acid bacterium *Lactobacillus plantarum*, and a propionic acid bacterium *Propionibacterium shermanii*.

Lactobacillus plantarum grows on glucose and produces lactic acid. *Propionibacterium shermanii* takes lactate (a salt of lactic acid) and metabolizes it to produce propionic acid and carbon dioxide. Although this is a model for commensalism, a (+,0) interaction, the resulting framework can easily be extended to mutualism (which can be found in works by Meyer *et al.*, [27] 1975; Miura *et al.*, [28] and Dean [6]). Lee *et al*'s model can be written as

$$\frac{dS}{dT} = D(S_i - S) - \frac{1}{Y_1} \frac{\mu_1 S N_1}{K_1 + S} - cN_1, \quad (3.1a)$$

$$\frac{dN_1}{dT} = \frac{\mu_1 S N_1}{K_1 + S} - DN_1, \quad (3.1b)$$

$$\frac{dP}{dT} = a \frac{\mu_1 S N_1}{K_1 + S} + bN_1 - \frac{1}{Y_2} \frac{\mu_1 P N_2}{K_2 + P} - DP, \quad (3.1c)$$

$$\frac{dN_2}{dT} = \frac{\mu_1 P N_2}{K_2 + P} - DN_2, \quad (3.1d)$$

where S is the substrate (glucose), P is the product (lactate), N_1 is the density of *Lactobacillus plantarum*, and N_2 is the density of *Propionibacterium shermanii*. The model contains the usual dilution rate, inflowing substrate concentration, functional responses, half-saturation constants. The two terms cN_1 and bN_1 account of *Lactobacillus plantarum*'s large maintenance cost. (*Lactobacillus plantarum* must consume glucose without growing in order to stay viable [16].) This model is very specific, in the next section we look at a more generalised way to make our mutualism models more realistic.

3.2 A Model that limits per capita birth and death rates

An example of the approach of constructing a model that limits the per capita birth and death rate can be found in the work of Wolin and Lawler [37]. They began by considering a single-species (N_1) population model in which the per capita birth rate (\tilde{b}) decreases with density,

$$\tilde{b} = b_0 - bN_1, \quad (3.2)$$

and the per capita death rate (\tilde{d}) increases with density,

$$\tilde{d} = d_0 + dN_1, \quad (3.3)$$

where b_0 and d_0 represent the maximum birth and death rate respectively and . The growth rate of the population N_1 is therefore the per capita death rate subtracted from the per capita birth rate multiplied by the population at time t , i.e.

$$\frac{dN_1}{dt} = (\tilde{b} - \tilde{d}) N_1 \quad (3.4)$$

substituting (3.2) and (3.3) into (3.4), we obtain

$$\frac{dN_1}{dt} = \left((b_0 - bN_1) - (d_0 + dN_1) \right) N_1$$

which expands to

$$\frac{dN_1}{dt} = b_0N_1 - bN_1^2 - d_0N_1 - dN_1^2$$

taking out factors of N_1 and N_1^2 gives us

$$\frac{dN_1}{dt} = (b_0 - d_0)N_1 - (b + d)N_1^2. \quad (3.5)$$

We notice that (3.5) is simply the logistic differential equation,

$$\frac{dN_1}{dt} = rN_1 - \frac{r}{K}N_1^2, \quad (3.6)$$

with

$$r = b_0 - d_0, \quad K = \frac{b_0 - d_0}{b + d}.$$

Now, let's assume that a facultative mutualist N_2 increases the per capita birth rate of N_1 , we add mN_2 to (3.2) where $m \in \mathbb{R}$ is some mutualistic constant

$$\tilde{b} = b_0 - bN_1 + mN_2, \quad (3.7)$$

but has no effect on the per capita death rate,

$$\tilde{d} = d_0 + dN_1, \quad (3.8)$$

so again, by substituting into (3.4) we get

$$\begin{aligned}
 \frac{dN_1}{dt} &= \left((b_0 - bN_1 + mN_2) - (d_0 + dN_1) \right) N_1 \\
 &= (b_0 - bN_1 + mN_2 - d_0 - dN_1) N_1 \\
 &= b_0N_1 - bN_1^2 + mN_1N_2 - d_0N_1 - dN_1^2 \\
 &= (b_0 - d_0)N_1 - (b - d)N_1^2 + mN_1N_2,
 \end{aligned}$$

taking out a factor of N_1 we can rearrange this to get an equation in the form

$$\frac{dN_1}{dt} = \frac{r}{K} N_1 \left(K - N_1 + \frac{mK}{r} N_2 \right) \quad (3.9)$$

where again

$$r = b_0 - d_0, \quad K = \frac{b_0 - d_0}{b + d}.$$

We notice that replacing $\frac{mK}{r}$ with α then (3.9) takes the form of the equations of the system (2.4a) - (2.4b), a model we have already deemed to be unrealistic. A further reason that this route is an unwise one to take is that equation (3.7) implies that the presence of many mutualists will raise the per capita birth rate above b_0 . However, since b_0 is the maximum per capita birth rate, this cannot happen therefore we cannot continue with this idea; we must approach the situation in a different way.

Let us imagine, instead, that the mutualism decreases the density dependence in the per capita birth rate of N_1 , as follows

$$\tilde{b} = b_0 - \frac{b}{1 + \alpha_{12}N_2} N_1, \quad (3.10)$$

substituting this into (3.4);

$$\begin{aligned}
 \frac{dN_1}{dt} &= \left(b_0 - \frac{b}{1 + \alpha_{12}N_2} N_1 - d_0 - dN_1 \right) N_1 \\
 &= \left((b_0 - d_0) - \frac{b}{1 + \alpha_{12}N_2} N_1 - dN_1 \right) N_1
 \end{aligned}$$

letting $r = b_0 - d_0$ again we arrive at the equation

$$\frac{dN_1}{dt} = \left(r - \frac{bN_1}{1 + \alpha_{12}N_2} - dN_1 \right) N_1.$$

By making a similar assumption with regard to the second species and adding appropriate subscripts to each unsubscripted b , d and r , we derive the system

$$\frac{dN_1}{dt} = \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) N_1 \quad (3.11a)$$

$$\frac{dN_2}{dt} = \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1} - d_2 N_2 \right) N_2 \quad (3.11b)$$

where

$$K_1 = \frac{r_1}{b_1 + d_1}, \quad K_2 = \frac{r_2}{b_2 + d_2}. \quad (3.12)$$

This is the model that we shall focus on throughout the rest of this paper.

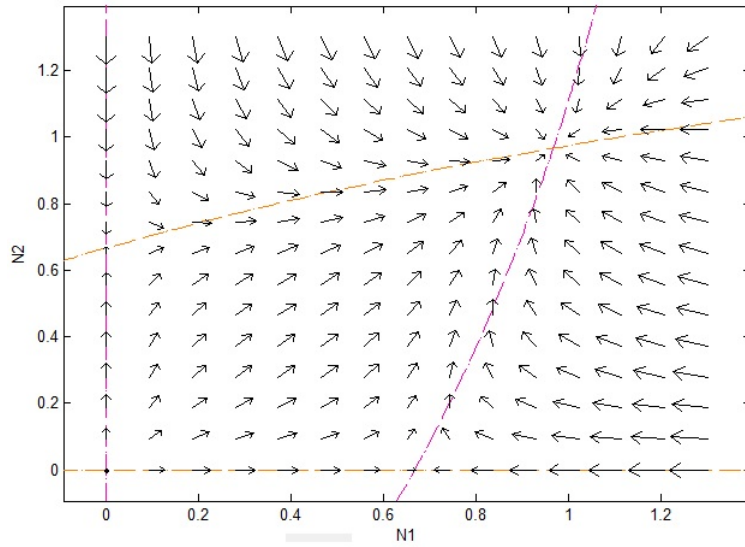


Figure 3.1: Bent zero-growth isoclines with parameter values $r_1 = r_2 = b_1 = b_2 = 1$, $\alpha_{12}, \alpha_{21} = 0.9$, $d_1 = d_2 = 0.5$

Let's find the non-trivial equilibrium point for this system. Consider equation (3.11a), by setting $\frac{dN_1}{dt} = 0$ we get

$$\left(r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^* \right) N_1^* = 0$$

so either

$$N_1^* = 0 \quad \text{or} \quad r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^* = 0.$$

We are looking for the non-trivial point, so we choose

$$r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^* = 0$$

removing a factor of N_1^* , we obtain

$$r_1 - N_1^* \left(\frac{b_1}{1 + \alpha_{12}N_2^*} + d_1 \right) = 0.$$

Since $d_1 = \frac{d_1(1+\alpha_{12}N_2^*)}{1+\alpha_{12}N_2^*}$, we derive

$$\begin{aligned} N_1^* \left(\frac{b_1}{1 + \alpha_{12}N_2^*} + \frac{d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right) &= r_1 \\ \Rightarrow N_1^* \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right) &= r_1 \\ \therefore N_1^* &= \frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)}. \end{aligned}$$

Similarly, we can use (3.11b) to find that

$$N_2^* = \frac{r_2(1 + \alpha_{21}N_1^*)}{b_2 + d_2(1 + \alpha_{21}N_1^*)}.$$

Therefore, our non-trivial equilibrium point for the system (3.11a) - (3.11b) is

$$(N_1^*, N_2^*) = \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)}, \frac{r_2(1 + \alpha_{21}N_1^*)}{b_2 + d_2(1 + \alpha_{21}N_1^*)} \right),$$

as illustrated by the intersecting point of the two zero-growth isoclines in figure 3.1.

3.2.1 Confirmation of computational work through a worked example

We have the equation

$$N_1^* = \frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)}.$$

Let us confirm that the graph created from MATLAB is correct by inputting the following parameter values $r_1 = r_2 = b_1 = b_2 = 1$, $\alpha_{12}, \alpha_{21} = 0.9$, $d_1 = d_2 = 0.5$. We get

$$N_1^* = \frac{1(1 + 0.9N_2^*)}{1 + 0.5(1 + 0.9N_2^*)}$$

by setting $N_2^* = 0$, we can find a numerical value for N_1^*

$$\begin{aligned} N_1^* &= \frac{1(1 + 0.9 \times 0)}{1 + 0.5(1 + 0.9 \times 0)} \\ &= \frac{1}{1.5} \\ &= 0.6 \end{aligned}$$

by referring to figure 3.1 we see that the zero-growth isocline for N_1^* (displayed as a pink line) crosses the N_1 -axis at this value. We can show in a similar manner that the N_2^* isocline will cross the N_2 -axis at the same value.

This confirms our computational work.

Chapter 4

Delay differential equations

4.1 Introduction to delay differential equations

4.1.1 What are DDEs?

Delay differential equations (DDEs) are equations of the form

$$y'(t) = f(t, y(t), y(t - \tau_1(t, y(t))), y(t - \tau_2(t, y(t))), \dots), \quad (4.1)$$

where the values τ_i , $i = 1, 2, \dots$ are delays that are measurable physical quantities and may be either constant, a function of t or a function of t and y itself. There are many similarities between the theory of ODEs and that of DDEs and analytical methods for ODEs have been extended to DDEs when possible. However, their differences have made new approaches necessary [23]. Delays cause severe mathematical complications and by the same token make a much richer range of phenomena possible [11].

4.1.2 Differences between ODEs and DDEs

An ordinary differential equation assumes that the effect of any changes to the system are instantaneous whereas a delay differential equation takes past history into account when dealing with such effects, ODEs generate a system that is finite dimensional, however DDEs generates a system that is infinite dimensional. Also in terms of solving the equations, ODEs require an initial value and DDEs require an initial function in order to determine a particular solution. An advantage of DDEs is that they enable a more accurate reflection of the system being modelled than ODEs, however the analytical theory is less well developed in DDEs than ODEs. [23]

4.2 Why are DDEs useful in modelling?

When modelling using mathematics, we of course want to represent the real world as best we can. With this in mind we notice that in some if not most situations, there is a time-lag between the inception of an action and the resulting change. Even though ordinary differential equations have been used as a fundamental tool of mathematical modellers for a very long time. An ODE model formulation of a system does not take in to account the presence of any delays. Formulation of a functional differential equation, which includes all ODEs, DDEs, FDEs (fractional differential equations), etc enables both the current and all previous values of a function and/or its derivatives to be considered when determining the future behaviour of a system. This often leads to an improved model.

Use of delays are sought in the modelling many situations, for example, in everyday occurrences;

- Pressing the 'on' button on a remote control \Rightarrow The television turning on
- Shower tap being turned \Rightarrow Water temperature change.
- Driver applying the brakes in a car \Rightarrow Car physically slowing down

In biology, there are also many examples in which delays take place;

- Foreign cells in the blood stream \Rightarrow White blood cells being produced
- Alcohol consumption \Rightarrow Consumer feeling the effects.
- Pain stimuli \Rightarrow Pain registering in the brain.

In our particular case, working with population dynamics. There are a large number of cases in which a time-lag must be taken into account. For example

- Seeds being planted \Rightarrow Seeds growing into pollenating plants.
- Animals being born \Rightarrow Animals developing into adults capable of reproduction.

If acquisition of food caused immediate birth of fully mature adults instead of merely producing eggs which develop into adults later on, then a system like $f(N) = r \left(1 - \frac{N}{K}\right)$ would be non-oscillatory. It would simply wander around its carrying capacity as a stochastic logistic process. The time-lag τ between appearance of eggs and adults is therefore fundamental to the observed process. However, whilst understanding the underlying biology may be described as fairly easy, translation of these biological ideas into mathematical equations is not so simple [31].

The size of the delay relative to the underlying time-scales influences the modellers decision about the choice of model formulation. Systems for which a model based on a functional differential equation is more appropriate than one based on an ODE can be referred to as problems with memory. A delay differential equation model may also be used to approximate a high dimensional model without delay by a lower dimensional model with delay, the analysis of which is more readily carried out. This approach has been used extensively in process control industry [23]

4.3 Constructing and solving the Verhulst-Pearl logistic equation

The following extract is taken from an MSc mathematical modelling coursework done by A. Rowntree [34]. It shows an example of how delays can be added into a well-known ecological model.

Definition 4 (Natural Period of a system). If the growth of a species in the absence of regulation obeys the equation $\frac{dN(t)}{dt} = rN(t)$ then the 'natural period' of the system is $\frac{1}{r}$.

In general if the feedback loop is longer than the 'natural period' of the system, then large amplitude oscillations will result. [31]

Let's construct a model to represent a situation in which the net growth rate per individual, denoted by $f(N)$, is a function of the total population size $N(t)$. Then the deterministic rate of increase is represented by the equation

$$\frac{dN}{dt} = Nf(N). \quad (4.2)$$

Now when N is large $\frac{df(N)}{dN}$ must be negative, since the larger the population becomes the greater must be its inhibitory effect on further growth. The simplest assumption to make is that $f(N)$ is linear, that is

$$f(N) = r - sN \quad (4.3)$$

for some positive constants r and s . Substituting (4.3) into (4.2) gives us

$$\frac{dN}{dt} = N(r - sN), \quad (4.4)$$

this is known as the Verhulst-Pearl logistic equation.

An alternative argument is to let r denote the intrinsic rate of natural increase for growth (the rate at which a population increases in size if there are no density-dependent forces regulating the population), and to let K be the carrying capacity. Then when N is near 0 and K we require $f(N)$ to be near r and 0 respectively. So let's consider

$$f(N) = r \left(1 - \frac{N}{K}\right) \quad (4.5)$$

which drops linearly as N increases. Substituting (4.5) into (4.2) we get

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right). \quad (4.6)$$

Now let's solve equation (4.6). Separation of variables yields

$$\frac{dN}{N \left(1 - \frac{N}{K}\right)} = r dt. \quad (4.7)$$

We can use partial fractions to separate the LHS of (4.7)

$$\frac{dN}{N \left(1 - \frac{N}{K}\right)} = \frac{A}{N} + \frac{B}{\left(1 - \frac{N}{K}\right)} \quad (4.8)$$

giving all terms a common denominator gives us

$$\begin{aligned} \Rightarrow \quad \frac{dN}{N \left(1 - \frac{N}{K}\right)} &= \frac{A \left(1 - \frac{N}{K}\right)}{N \left(1 - \frac{N}{K}\right)} + \frac{BN}{N \left(1 - \frac{N}{K}\right)} \\ \therefore \quad dN &= A \left(1 - \frac{N}{K}\right) + BN \end{aligned}$$

$$\begin{aligned}
\text{Let } N &= 0 \\
\Rightarrow A &= dN \\
\text{Let } \left(1 - \frac{N}{K}\right) &= 0 \therefore K = N \\
\Rightarrow B &= \frac{dN}{K}.
\end{aligned}$$

So, substituting our expressions for A and B back into equation (4.8) gives us

$$\frac{dN}{N \left(1 - \frac{N}{K}\right)} = \frac{dN}{N} + \frac{dN}{K \left(1 - \frac{N}{K}\right)} \quad (4.9)$$

therefore by (4.7), (4.9) becomes

$$\frac{dN}{N} + \frac{dN}{K \left(1 - \frac{N}{K}\right)} = r dt. \quad (4.10)$$

Integrating both sides of (4.10), we get

$$\begin{aligned}
\int \frac{1}{N} dN + \frac{1}{K} \int \frac{1}{\left(1 - \frac{N}{K}\right)} dN &= \int r dt \\
\ln(N) - \ln\left(1 - \frac{N}{K}\right) &= rt + C
\end{aligned}$$

using laws of logs on the LHS we get

$$\ln\left(\frac{N}{\left(1 - \frac{N}{K}\right)}\right) = rt + C.$$

Taking the exponential of both sides;

$$\begin{aligned}
\frac{N}{1 - \frac{N}{K}} &= e^{rt+C} \\
\frac{N}{1 - \frac{N}{K}} &= \mu e^{rt}
\end{aligned}$$

where $\mu = e^C$,

$$\begin{aligned}
\Rightarrow N &= \mu e^{rt} \left(1 - \frac{N}{K}\right) \\
N &= \mu e^{rt} - \mu e^{rt} \left(\frac{N}{K}\right)
\end{aligned}$$

Rearranging further for N gives us our general solution of (4.6)

$$N(t) = \frac{\mu e^{rt}}{\left(1 + \frac{\mu e^{rt}}{K}\right)} \quad (4.11)$$

We can eliminate our constant of integration μ by letting $t = 0$ and $N(0) = N_0$ be our initial condition, this gives us

$$\mu = \frac{N_0}{k - N_0} \quad (4.12)$$

Substituting (4.12) into (4.11) gives us a particular solution to (4.6)

$$N(t) = \frac{N_0 e^{rt}}{(K - N_0) \left(1 + \frac{N_0 e^{rt}}{(k - N_0)K}\right)}. \quad (4.13)$$

4.4 Adding a delay term to equation (4.6)

Introducing a delay term τ to equation (4.6) gives us

$$\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t - \tau)}{K}\right) \quad (4.14)$$

The delay differential equation (4.14) can now be used to model the dynamics of a single species population growing towards K with a constant reproduction rate r ; the term $\left(1 - \frac{N(t - \tau)}{K}\right)$ denotes a density dependent feedback mechanism which takes τ units of time to respond to changes in the population density represented in the equation by N .

By a change of variables in the following manner; let $N(t) = Ky(t)$, $\alpha = r\tau$ and $t = s\tau$, (4.14) can be brought to an equation in the dimensionless form

$$\frac{dy(s)}{ds} = -\alpha y(s - 1) (1 + y(s)) \quad (4.15)$$

where α is a positive constant that represents the ratio of delay to growth time [11, 9]. Equation (4.15) has been studied in depth by a number of authors, notably Kakutani and Markus [15] and Wright [38]

This is a good example of how delays can be introduced to significant equations, we shall take note of these techniques in the next chapter when we introducing delays to the model (3.11a) - (3.11b).

Chapter 5

Introducing delays to the model (3.11a) - (3.11b)

The next several chapters follows the work done by Joharee and Roberts [32], however, we have elongated and elucidated proofs and methods used to provide a more thorough explanation of the mathematics occurring¹.

Considering the model (3.11a) - (3.11b)

$$\begin{aligned}\frac{dN_1}{dt} &= \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) N_1 \\ \frac{dN_2}{dt} &= \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1} - d_2 N_2 \right) N_2,\end{aligned}$$

we can introduce a delay into the equations to reflect the idea that mutualistic effects on the population are not realised instantaneously, the model now takes the following form

$$\frac{dN_1}{dt} = \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 N_1 \right) N_1 \quad (5.1a)$$

$$\frac{dN_2}{dt} = \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1(t - \tau_1)} - d_2 N_2 \right) N_2, \quad (5.1b)$$

in order to obtain a specific solution, this model must be coupled with a pair of initial functions;

$$N_1(t) = \xi_1(t) \quad \text{for} \quad -\tau_1 \leq t \leq 0, \quad (5.2a)$$

$$N_2(t) = \xi_2(t) \quad \text{for} \quad -\tau_2 \leq t \leq 0, \quad (5.2b)$$

where each initial function is differentiable over its domain and that its range be the set of positive real numbers. In this chapter, we shall try to prove that the system (5.1a) - (5.1b) displays asymptotic stability, however before we can do this we must prove the following inequality is true.

¹When studying this paper, a number of discrepancies in the form of typing errors were found, corrections have been made for this dissertation.

Lemma 5.1. If $r_1, r_2, b_1, b_2, d_1, d_2 \in (0, \infty)$, $\alpha_{12}, \alpha_{21} \in [1, \infty)$ then

$$\frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} < r_1r_2 \quad (5.3)$$

Proof. When finding the non-trivial equilibrium point, we ignore the delay aspect of (5.1a) - (5.1b) as it has no bearing on our equilibrium. Hence we obtain the same point as the system (3.11a) - (3.11b), we can refer back to Chapter 3 to recall the process of finding it. Recall that

$$E = (N_1^*, N_2^*) = \left(\frac{r_1(1+\alpha_{12}N_2^*)}{b_1+d_1(1+\alpha_{12}N_2^*)}, \frac{r_2(1+\alpha_{21}N_1^*)}{b_2+d_2(1+\alpha_{21}N_1^*)} \right)$$

Note that multiplying N_1^* by N_2^* , we get

$$N_1^*N_2^* = \frac{r_1r_2(1+\alpha_{12}N_2^*)(1+\alpha_{21}N_1^*)}{(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))} \quad (5.4)$$

and solving for r_1r_2 gives us

$$r_1r_2 = \frac{N_1^*N_2^*(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))}{(1+\alpha_{12}N_2^*)(1+\alpha_{21}N_1^*)}. \quad (5.5)$$

Since $b_1, b_2, d_1, d_2 \in (0, \infty)$, $\alpha_{12}, \alpha_{21} \in [1, \infty)$ and $(N_1^*, N_2^*) \neq (0, 0)$ it is clear to see that

$$b_1 < b_1 + d_1(1+\alpha_{12}N_2^*) \quad \text{and} \quad b_2 < b_2 + d_2(1+\alpha_{21}N_1^*), \quad (5.6)$$

therefore it follows from (5.6) that

$$\begin{aligned} & \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} \\ & < \frac{\alpha_{12}\alpha_{21}(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} \end{aligned} \quad (5.7)$$

is true. For the sake of simplicity let

$$\Theta = \frac{\alpha_{12}\alpha_{21}(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2}.$$

Therefore by substituting the value for $N_1^*N_2^*$ from equation (5.4) into the RHS of (5.7) we get

$$\begin{aligned} \Theta &= \left(\frac{\alpha_{12}\alpha_{21}(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} \right) \\ &\quad \times \left(\frac{r_1r_2(1+\alpha_{12}N_2^*)(1+\alpha_{21}N_1^*)}{(b_1+d_1(1+\alpha_{12}N_2^*))(b_2+d_2(1+\alpha_{21}N_1^*))} \right)^2 \end{aligned}$$

which simplifies to the single fraction

$$\Theta = \frac{\alpha_{12}\alpha_{21} (r_1 r_2)^2 (1 + \alpha_{12}N_2^*)^2 (1 + \alpha_{21}N_1^*)^2 (b_1 + d_1 (1 + \alpha_{12}N_2^*)) (b_2 + d_2 (1 + \alpha_{21}N_1^*))}{(1 + \alpha_{12}N_2^*)^2 (1 + \alpha_{21}N_1^*)^2 (b_1 + d_1 (1 + \alpha_{12}N_2^*))^2 (b_2 + d_2 (1 + \alpha_{21}N_1^*))^2}$$

cancelling gives us

$$\Theta = \frac{\alpha_{12}\alpha_{21} (r_1 r_2)^2}{(b_1 + d_1 (1 + \alpha_{12}N_2^*)) (b_2 + d_2 (1 + \alpha_{21}N_1^*))} \quad (5.8)$$

removing $1 \times r_1 r_2$ from (5.8) we get

$$\Theta = \frac{\alpha_{12}\alpha_{21} r_1 r_2}{(b_1 + d_1 (1 + \alpha_{12}N_2^*)) (b_2 + d_2 (1 + \alpha_{21}N_1^*))} (r_1 r_2) \quad (5.9)$$

we now replace the $r_1 r_2$ that has been taken out of the fraction with the expression for $r_1 r_2$ found in equation (5.5);

$$\begin{aligned} \Theta = & \left(\frac{\alpha_{12}\alpha_{21} r_1 r_2}{(b_1 + d_1 (1 + \alpha_{12}N_2^*)) (b_2 + d_2 (1 + \alpha_{21}N_1^*))} \right) \\ & \times \left(\frac{N_1^* N_2^* (b_1 + d_1 (1 + \alpha_{12}N_2^*)) (b_2 + d_2 (1 + \alpha_{21}N_1^*))}{(1 + \alpha_{12}N_2^*) (1 + \alpha_{21}N_1^*)} \right) \end{aligned}$$

cross-cancelling gives us a more simple fraction

$$\Theta = \frac{\alpha_{12}\alpha_{21} r_1 r_2 N_1^* N_2^*}{(1 + \alpha_{12}N_2^*) (1 + \alpha_{21}N_1^*)}$$

that can be rearranged to

$$\Theta = r_1 r_2 \left(\frac{\alpha_{12}N_2^*}{1 + \alpha_{12}N_2^*} \right) \left(\frac{\alpha_{21}N_1^*}{1 + \alpha_{21}N_1^*} \right).$$

Now, since we know that

$$\alpha_{12}, \alpha_{21} \in [1, \infty) \text{ and } (N_1^*, N_2^*) \neq (0, 0)$$

this implies that

$$\left(\frac{\alpha_{12}N_2^*}{1 + \alpha_{12}N_2^*} \right), \left(\frac{\alpha_{21}N_1^*}{1 + \alpha_{21}N_1^*} \right) \in (0, 1).$$

Therefore it is clear to see that

$$\frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} = r_1r_2 \left(\frac{\alpha_{12}N_2^*}{1+\alpha_{12}N_2^*} \right) \left(\frac{\alpha_{21}N_1^*}{1+\alpha_{21}N_1^*} \right) < r_1r_2$$

holds true, hence the proof of the lemma (5.3) is completed. \square

Next, let's introduce some preliminary to characteristic equations and stability theory.

5.1 Preliminaries

5.1.1 Characteristic equations with regard to delays

Characteristic equations are used in the process of determining a system's stability. Throughout the remainder of this chapter, we will notice that the characteristic equations for the delay model differ to those of our ODE model. It is mentioned by Kuang [17] that as with linear ODEs, stability properties of linear DDEs can be characterised and analysed by studying their characteristic equations. For example, the characteristic equation for $x'(t) = ax(t) + bx(t - \tau)$ is $\lambda - a - be^{-\lambda\tau} = 0$. The roots λ of the characteristic equation are called characteristic roots. Notice that the root appears in the exponent of the last term in the characteristic equation, causing the characteristic equation to possess an infinite number of roots [18]. We shall use this information when determining the asymptotic stability of our delay model.

5.1.2 A note on asymptotic stability

It is written in Braun (1993) [4] that

"...suppose a vector-valued function

$$\frac{g(x)}{\|x\|} \equiv \frac{g(x)}{\max\{|x_1|, \dots, |x_n|\}}$$

is a continuous function of x_1, \dots, x_n which vanishes for $x = 0$. Then, the equilibrium solution $x(t) \equiv 0$ of $\frac{dx}{dt} = Ax + g(x)$ is asymptotically stable if the equilibrium solution $x(t) \equiv 0$ of the linearised equation $\frac{dx}{dt} = Ax$ is asymptotically stable. **Equivalently, the solution $x(t) \equiv 0$ of $\frac{dx}{dt} = Ax + g(x)$ is asymptotically stable if all the eigenvalues of A have negative real part...."**

Now, we are not interested in linearising our system, so let's focus on the second part of this text which is on bold. We can now state and prove the following stability theorem.

5.2 Stability of the DDE

Theorem 5.1. Assume that $r_1, r_2, b_1, b_2, d_1, d_2 \in (0, \infty)$, $\alpha_{12}, \alpha_{21} \in [1, \infty)$. Then the positive steady state $E = (N_1^*, N_2^*)$ of the delay differential system (5.1a) - (5.1b) with initial functions (5.2a) - (5.2b) is asymptotically stable

Proof. Recall again that our on-trivial equilibrium point is

$$E = (N_1^*, N_2^*) = \left(\frac{r_1 (1 + \alpha_{12} N_2)}{b_1 + d_1 (1 + \alpha_{12} N_2)}, \frac{r_2 (1 + \alpha_{21} N_1)}{b_2 + d_2 (1 + \alpha_{21} N_1)} \right).$$

Let us construct the Jacobian matrix (see Appendix A) of our system (5.1a) - (5.1b). Firstly by defining the new functions f_2 and g_2 as

$$\begin{aligned} \frac{dN_1}{dt} &= \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 N_1 \right) N_1 = f_2(N_1, N_2) \\ \frac{dN_2}{dt} &= \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1(t - \tau_1)} - d_2 N_2 \right) N_2 = g_2(N_1, N_2). \end{aligned}$$

Next we calculate the following partial derivatives $\frac{\partial f_2}{\partial N_1}$, $\frac{\partial f_2}{\partial N_2}$, $\frac{\partial g_2}{\partial N_1}$ and $\frac{\partial g_2}{\partial N_2}$ that shall become the elements in our Jacobian matrix

$$J = \begin{pmatrix} \frac{\partial f_2}{\partial N_1} & \frac{\partial f_2}{\partial N_2} \\ \frac{\partial g_2}{\partial N_1} & \frac{\partial g_2}{\partial N_2} \end{pmatrix}.$$

Firstly, for $\frac{\partial f_2}{\partial N_1}$ and $\frac{\partial g_2}{\partial N_2}$

$$\frac{\partial f_2}{\partial N_1} = \frac{\partial}{\partial N_1} \left(\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 N_1 \right) N_1 \right).$$

Using the product rule²

$$\begin{aligned} \frac{\partial f_2}{\partial N_1} &= \left(\frac{b_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 \right) N_1 + \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 N_1 \right) \times 1 \\ &= r_1 - 2N_1 \left(\frac{b_1}{1 + \alpha_{12} N_2(t - \tau_2)} + d_1 \right) \end{aligned}$$

hence

$$\frac{\partial f_2}{\partial N_1} = r_1 - 2N_1 \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2(t - \tau_2))}{1 + \alpha_{12} N_2(t - \tau_2)} \right).$$

Similarly we can show that

$$\frac{\partial g_2}{\partial N_2} = r_2 - 2N_2 \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1(t - \tau_1))}{1 + \alpha_{21} N_1(t - \tau_1)} \right).$$

Next, for $\frac{\partial f_2}{\partial N_2}$ and $\frac{\partial g_2}{\partial N_1}$ we have

$$\frac{\partial f_2}{\partial N_2} = \frac{\partial}{\partial N_2} \left(\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2(t - \tau_2)} - d_1 N_1 \right) N_1 \right)$$

Using the product rule

$$\frac{\partial f_2}{\partial N_2} = \left(0 - b_1 N_1 \times \frac{\partial}{\partial N_2} \left(\frac{1}{1 + \alpha_{12} N_2 (t - \tau_2)} \right) - 0 \right) N_1 + \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2 (t - \tau_2)} - d_1 N_1 \right) \times 0$$

$$\frac{\partial f_2}{\partial N_2} = -b_1 N_1^2 \times \frac{\partial}{\partial N_2} \left(\frac{1}{1 + \alpha_{12} N_2 (t - \tau_2)} \right)$$

removing constants from the differential gives us

$$\begin{aligned} \frac{\partial f_2}{\partial N_2} &= -b_1 N_1^2 (-\alpha_{12}) \left(\frac{1}{(1 + \alpha_{12} N_2 (t - \tau_2))^2} \right) \times \frac{\partial}{\partial N_2} N_2 (t - \tau_2) \\ \Rightarrow \frac{\partial f_2}{\partial N_2} &= \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2 (t - \tau_2))^2} \times \frac{\partial}{\partial N_2} N_2 (t - \tau_2) \end{aligned}$$

hence

$$\frac{\partial f_2}{\partial N_2} = \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2 (t - \tau_2))^2} e^{-\lambda \tau_2}.$$

Similarly we can show that

$$\frac{\partial g_2}{\partial N_1} = \frac{\alpha_{21} b_2 N_2^2}{(1 + \alpha_{21} N_1 (t - \tau_1))^2} e^{-\lambda \tau_1}.$$

So, our Jacobian matrix takes the following form

$$J = \begin{pmatrix} r_1 - 2N_1 \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2 (t - \tau_2))}{1 + \alpha_{12} N_2 (t - \tau_2)} \right) & \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2 (t - \tau_2))^2} e^{-\lambda \tau_2} \\ \frac{\alpha_{21} b_2 N_2^2}{(1 + \alpha_{21} N_1 (t - \tau_1))^2} e^{-\lambda \tau_1} & r_2 - 2N_2 \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1 (t - \tau_1))}{1 + \alpha_{21} N_1 (t - \tau_1)} \right) \end{pmatrix}.$$

Now, we can construct the Jacobian matrix of the system evaluated at our equilibrium point $E = (N_1^*, N_2^*)$;

$$J_E = \begin{pmatrix} r_1 - 2N_1^* \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2^*)}{1 + \alpha_{12} N_2^*} \right) & \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^{-\lambda \tau_2} \\ \frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} e^{-\lambda \tau_1} & r_2 - 2N_2^* \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1^*)}{1 + \alpha_{21} N_1^*} \right) \end{pmatrix}.$$

The diagonal elements in the matrix J_E can be simplified as follows

$$\begin{aligned} r_1 - 2N_1^* \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2^*)}{1 + \alpha_{12} N_2^*} \right) &= r_1 - 2 \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2^*)}{1 + \alpha_{12} N_2^*} \right) \left(\frac{r_1 (1 + \alpha_{12} N_2)}{b_1 + d_1 (1 + \alpha_{12} N_2)} \right) \\ &= r_1 - 2r_1 \\ &= -r_1 \end{aligned}$$

and

$$\begin{aligned} r_2 - 2N_2^* \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1^*)}{1 + \alpha_{21} N_1^*} \right) &= r_2 - 2 \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1^*)}{1 + \alpha_{21} N_1^*} \right) \left(\frac{r_2 (1 + \alpha_{21} N_1)}{b_2 + d_2 (1 + \alpha_{21} N_1)} \right) \\ &= r_2 - 2r_2 \\ &= -r_2. \end{aligned}$$

So our the Jacobian matrix of the system evaluated at the equilibrium point E now looks like

$$J_E = \begin{pmatrix} -r_1 & \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^{-\lambda \tau_2} \\ \frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} e^{-\lambda \tau_1} & -r_2 \end{pmatrix}. \quad (5.10)$$

Using

$$(J_E - \lambda I) = \begin{pmatrix} -r_1 - \lambda & \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^{-\lambda \tau_2} \\ \frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} e^{-\lambda \tau_1} & -r_2 - \lambda \end{pmatrix}, \quad (5.11)$$

we can now find our characteristic equation by

$$\begin{aligned}
& \det(J_E - \lambda I) = 0 \\
\Rightarrow & \det \begin{pmatrix} -r_1 - \lambda & \frac{\alpha_{12}b_1(N_1^*)^2}{(1+\alpha_{12}N_2^*)^2}e^{-\lambda\tau_2} \\ \frac{\alpha_{21}b_2(N_2^*)^2}{(1+\alpha_{21}N_1^*)^2}e^{-\lambda\tau_1} & -r_2 - \lambda \end{pmatrix} = 0 \\
\Rightarrow & \left(\lambda^2 + (r_1 + r_2)\lambda + r_1r_2 \right) - \left(\frac{\alpha_{12}b_1(N_1^*)^2}{(1+\alpha_{12}N_2^*)^2}e^{-\lambda\tau_2} \right) \left(\frac{\alpha_{21}b_2(N_2^*)^2}{(1+\alpha_{21}N_1^*)^2}e^{-\lambda\tau_1} \right) = 0 \\
\Rightarrow & \lambda^2 + (r_1 + r_2)\lambda + r_1r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*)^2(N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2}e^{-\lambda(\tau_1+\tau_2)} = 0, \tag{5.12}
\end{aligned}$$

which, for convenience we shall write (5.12) as

$$\lambda^2 + A\lambda + B - Ce^{-\lambda\tau} = 0, \tag{5.13}$$

where

$$A = r_1 + r_2 \tag{5.14}$$

$$B = r_1r_2 \tag{5.15}$$

$$C = \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*)^2(N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} \tag{5.16}$$

$$\tau = \tau_1 + \tau_2. \tag{5.17}$$

Our equilibrium point E is asymptotically stable if the roots of the characteristic equation (5.13) have negative real part³.

Substituting $\lambda = x + iy$ into (5.13) gives us

$$(x + iy)^2 + A(x + iy) + B - Ce^{-(x+iy)\tau} = 0$$

which expands to

$$x^2 + 2ixy - y^2 + Ax + Aiy + B - C(e^{-x\tau}\cos(y\tau) - ie^{-iy\tau}\sin(y\tau)) = 0. \tag{5.18}$$

Separating real and imaginary part of (5.18) yields the following two equations

³It is well known that if the characteristic equation associated with a linear neutral equation has roots only with negative real parts, and if all the roots are uniformly bounded away from the imaginary axis, then the trivial solution of the linear neutral equation is uniformly asymptotically stable [17]. We also refer back to our preliminary at the start of this chapter.

$$\text{Real} \Rightarrow (x^2 - y^2) + (Ax + B) = Ce^{-x\tau} \cos(y\tau) \quad (5.19)$$

$$\text{Imaginary} \Rightarrow 2xy + Ay = -Ce^{-x\tau} \sin(y\tau). \quad (5.20)$$

Squaring and adding (5.19) - (5.20) we get

$$((x^2 - y^2) + (Ax + B))^2 + (2xy + Ay)^2 = (Ce^{-x\tau} \cos(y\tau))^2 + (-Ce^{-x\tau} \sin(y\tau))^2$$

which expands to

$$\begin{aligned} & x^4 - x^2y^2 + x^3A + x^2B - x^2y^2 + y^4 - xy^2A - y^2B + x^3A - xy^2A + x^2A^2 + xAB \\ & + x^2B - y^2B + xAB + B^2 + 4x^2y^2 + 2Axy^2 + 2Axy^2 + A^2y^2 \\ & - C^2e^{-2x\tau} (\cos^2(y\tau) + \sin^2(y\tau)) = 0. \end{aligned}$$

Simplifying terms gives us

$$x^4 + 2x^2y^2 + y^4 + x^2A^2 + 2xy^2A + A^2y^2 - 2y^2B + 2x^3A + 2x^2B + 2xAB + B^2 - C^2e^{-2x\tau} = 0$$

which can now be factorised into the following equation

$$(x^2 + y^2)^2 + x^2A^2 + y^2(2xA + A^2 - 2B) + 2x(x^2A + xB + AB) + B^2 \left(1 - \frac{C^2}{B^2}e^{-2x\tau}\right) = 0. \quad (5.21)$$

Using our Lemma (5.1), we have the additional information that

$$0 < \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} < r_1r_2$$

that is

$$0 < C < B \quad (5.22)$$

It is also clear that $AB > 0$ and $A^2 - 2B > B$. If we assume that $x \geq 0$ then (5.21) is only satisfied if $x = y = 0$ and $B = C$. This contradicts (5.22) and so $x = \text{Re}(\lambda) < 0$. Therefore we conclude that every root of the characteristic equation (5.13) has a negative real part and hence asymptotic stability of the equilibrium point E is confirmed. This concludes our proof. \square

Asymptotic stability of this system is not conditional on the delay, to show this we shall determine stability of the underlying ODE without delays.

5.3 Stability of the underlying ODE

Setting the delays $\tau_1, \tau_2 = 0$ we can confirm asymptotic stability of the underlying ordinary differential system in a similar manner, we have the system of equations f_3 and g_3

$$\begin{aligned}\frac{dN_1}{dt} &= \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) N_1 = f_3(N_1, N_2) \\ \frac{dN_2}{dt} &= \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1} - d_2 N_2 \right) N_2 = g_3(N_1, N_2)\end{aligned}$$

with equilibrium points

$$E = (N_1^*, N_2^*) = \left(\frac{r_1 (1 + \alpha_{12} N_2)}{b_1 + d_1 (1 + \alpha_{12} N_2)}, \frac{r_2 (1 + \alpha_{21} N_1)}{b_2 + d_2 (1 + \alpha_{21} N_1)} \right).$$

Again, calculating the following partial derivatives $\frac{\partial f_3}{\partial N_1}$, $\frac{\partial f_3}{\partial N_2}$, $\frac{\partial g_3}{\partial N_1}$ and $\frac{\partial g_3}{\partial N_2}$, as before

$$\frac{\partial f_3}{\partial N_1} = r_1 - 2N_1 \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2)}{1 + \alpha_{12} N_2} \right)$$

similarly,

$$\frac{\partial g_3}{\partial N_2} = r_2 - 2N_2 \left(\frac{b_2 + d_2 (1 + \alpha_{21} N_1)}{1 + \alpha_{21} N_1(t)} \right)$$

calculating $\frac{\partial f_3}{\partial N_2}$ is slightly different as there is no delay term to differentiate,

$$\frac{\partial f_3}{\partial N_2} = \frac{\partial}{\partial N_2} \left(\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) N_1 \right).$$

Using the product rule we get

$$\begin{aligned}\frac{\partial f_3}{\partial N_2} &= \left(0 - b_1 N_1 \times \frac{\partial}{\partial N_2} \left(\frac{1}{1 + \alpha_{12} N_2} \right) - 0 \right) N_1 + \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) \times 0 \\ &= -b_1 N_1^2 \times \frac{\partial}{\partial N_2} \left(\frac{1}{1 + \alpha_{12} N_2} \right).\end{aligned}$$

Using the chain rule, we arrive at

$$\frac{\partial f_3}{\partial N_2} = \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2)^2}$$

and again, we can show that

$$\frac{\partial g_3}{\partial N_1} = \frac{\alpha_{21} b_2 N_2^2}{(1 + \alpha_{21} N_1)^2}.$$

The Jacobian matrix takes the following form

$$J = \begin{pmatrix} r_1 - 2N_1 \left(\frac{b_1 + d_1(1 + \alpha_{12} N_2)}{1 + \alpha_{12} N_2} \right) & \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2)^2} \\ \frac{\alpha_{21} b_2 N_2^2}{(1 + \alpha_{21} N_1)^2} & r_2 - 2N_2 \left(\frac{b_2 + d_2(1 + \alpha_{21} N_1)}{1 + \alpha_{21} N_1} \right) \end{pmatrix}.$$

which, when evaluated at our equilibrium point simplifies to

$$J_E = \begin{pmatrix} -r_1 & \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} \\ \frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} & -r_2 \end{pmatrix}. \quad (5.23)$$

We can hence find our characteristic equation by

$$\begin{aligned} \det(J_E - \lambda I) &= 0 \\ \Rightarrow \det \begin{pmatrix} -r_1 - \lambda & \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2)^2} \\ \frac{\alpha_{21} b_2 N_2^2}{(1 + \alpha_{21} N_1)^2} & -r_2 - \lambda \end{pmatrix} &= 0 \\ \Rightarrow \left(\lambda^2 + (r_1 + r_2)\lambda + r_1 r_2 \right) - \left(\frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} \right) \left(\frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} \right) &= 0 \\ \Rightarrow \lambda^2 + (r_1 + r_2)\lambda + r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} &= 0 \end{aligned}$$

which can simplify to

$$\lambda^2 + A\lambda + (B - C) = 0 \quad (5.24)$$

where

$$A = r_1 + r_2$$

and

$$B - C = r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2}.$$

We can now solve our characteristic equation by using the quadratic formula. So we get

$$\lambda = \frac{-A \pm \sqrt{A^2 - 4(B - C)}}{2}$$

which yields two solutions

$$\lambda_1 = \frac{-A + \sqrt{A^2 - 4(B - C)}}{2}$$

and

$$\lambda_2 = \frac{-A - \sqrt{A^2 - 4(B - C)}}{2}.$$

To confirm asymptotic stability of the system, we must show that the real part of λ is negative i.e. to show that the real parts of both solutions λ_1 and λ_2 are negative.

Now, consider the discriminant⁴, let's call it Δ , if $\Delta > 0$ then there exists no imaginary part in the solution. So let's show this; We know that $A, B, C > 0$ and that $B > C$

$$\begin{aligned} \Delta &= A^2 - 4(B - C) \\ \Rightarrow \Delta &= (r_1 + r_2)^2 - 4 \left(r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \right) \\ \Rightarrow \Delta &= r_1^2 + 2r_1 r_2 + r_2^2 - 4r_1 r_2 + 4 \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \\ \Rightarrow \Delta &= r_1^2 - 2r_1 r_2 + r_2^2 + 4 \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \\ \Rightarrow \Delta &= (r_1 + r_2)^2 + 4 \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^*)^2 (N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \\ \therefore \Delta &> 0. \end{aligned}$$

⁴The discriminant of the quadratic formula is $b^2 - 4ac$ that is under the square root sign.

Now that we know $\Delta > 0$ then of course $\sqrt{\Delta} > 0$, so it is clear to see that $\lambda_2 < 0$. Next is to show that $\lambda_1 < 0$, which is essentially to show that

$$0 > -A + \sqrt{A^2 - 4(B - C)}. \quad (5.25)$$

We know that multiplying the RHS of (5.25) by $\frac{1}{2}$ will make no change to its sign. So,

$$0 > -A + \sqrt{A^2 - 4(B - C)}$$

$$A > \sqrt{A^2 - 4(B - C)}$$

$$A^2 > A^2 - 4(B - C)$$

$$0 > -4(B - C)$$

which holds true since $B > C$. Therefore $\lambda_1 < 0$ hence $\lambda < 0$ which of course implies that $\text{Re}(\lambda)$ since λ has no imaginary part. Asymptotic stability is now confirmed for our delay system in the special case of $\tau_1, \tau_2 = 0$.

Chapter 6

Discrete time models

6.1 Introduction to discrete time models

6.1.1 What is a discrete time model?

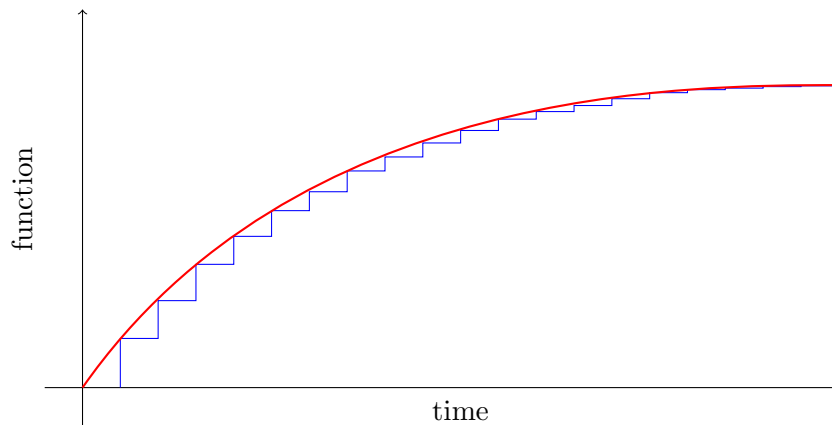


Figure 6.1: Graph showing continuous behaviour (red) compared with discrete behaviour (blue) of an arbitrary function of time

Dealing with discrete time is to think of time as occurring at distinct, separate points. The idea that time jumps from once point to the next is considered as opposed to the idea that time moves in a continuous manner. We can take the often used example of clocks to visualise this concept better, many analogue clocks have the minute and the hour hand moving around the face in a slow continuous circular motion whereas a digital clock will jump from say, 19:59pm to 18:00pm; each minute in the digital clock is a discrete time period. See figure 6.1 for an illustrative example of continuous behaviour versus discrete behaviour.

6.1.2 Why is a discrete model necessary in modelling population dynamics?

Often in nature, births of organisms occur during regular 'breeding seasons' that are mostly very specific. For example, many insects will reproduce during their lifespan and lay their eggs before they die. This leaves a period of time between generations.

Most models are considered to have a constant environment, meaning the model is assumed to be autonomous, that is, all biological and environmental parameters have been assumed to be constants in time. However, this is rarely the case in real life, because many of these parameters do in fact vary in time (naturally subject to seasonal fluctuations for example). When this is taken into account, a model must be nonautonomous. This is of course, more difficult analyse in general but in doing so, one can take advantage of those varying parameters [8]. It has been argued by Freedman [10] that the discrete time models governed by difference equations are more appropriate than the continuous ones with the populations have non-overlapping generations.

6.2 Discretising our mutualism model (3.11a) - (3.11b) using piecewise constant arguments

Let's start by proposing discrete analogues of the model (3.11a) - (3.11b) and use an approach described and applied in the work by Fan and Wang, 2002 [8]. In order to do this we take the system (3.11a) - (3.11b) which we recall after dividing both sides by N_1 and N_2 respectively looks like;

$$\begin{aligned}\frac{1}{N_1(t)} \frac{dN_1}{dt} &= r_1 - \frac{b_1 N_1(t)}{1 + \alpha_{12} N_2(t)} - d_1 N_1(t) \\ \frac{1}{N_2(t)} \frac{dN_2}{dt} &= r_2 - \frac{b_2 N_2(t)}{1 + \alpha_{21} N_1(t)} - d_2 N_2(t).\end{aligned}$$

We are going to discretise the RHS such that it takes the following form

$$\frac{1}{N_1(t)} \frac{dN_1}{dt} = r_1 - \frac{b_1 N_1([t])}{1 + \alpha_{12} N_2([t])} - d_1 N_1([t]) \quad (6.1a)$$

$$\frac{1}{N_2(t)} \frac{dN_2}{dt} = r_2 - \frac{b_2 N_2([t])}{1 + \alpha_{21} N_1([t])} - d_2 N_2([t]) \quad (6.1b)$$

where $[t]$ represents the integer part of t , $t \in (0, \infty)$. Equations of the type (6.1a) - (6.1b) are known as differential equations with piecewise constant arguments and these equations occupy a position midway between differential equations and difference equations [32].

On any interval $[k, k + 1]$, $k = 0, 1, 2, \dots$, we can integrate (6.1a):

$$\Rightarrow \int_k^t \frac{1}{N_1(t)} \frac{dN_1(t)}{dt} dt = \int_k^t \frac{dN_1}{N_1(t)} = \int_k^t \left(r_1 - \frac{b_1 N_1([t])}{1 + \alpha_{12} N_2([t])} - d_1 N_1([t]) \right) dt$$

$$\begin{aligned}
&\Rightarrow \int_k^t \frac{dN_1}{N_1(t)} = \int_k^t r_1 dt - \int_k^t \frac{b_1 N_1([t])}{1 + \alpha_{12} N_2([t])} dt - \int_k^t d_1 N_1([t]) dt \\
&\Rightarrow \left[\ln(N_1(t)) \right]_k^t = \left[r_1 t \right]_k^t - \left[\frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} t \right]_k^t - \left[d_1 N_1(k) t \right]_k^t \\
&\Rightarrow \ln(N_1(t)) - \ln(N_1(k)) = \left[(r_1 t) - (r_1 k) \right] - \left[\left(\frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} t \right) - \left(\left(\frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} k \right) \right) \right] \\
&\quad - \left[(d_1 N_1(k) t) - (d_1 N_1(k) k) \right] \\
&\Rightarrow \ln(N_1(t)) - \ln(N_1(k)) = r_1(t - k) - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)}(t - k) - d_1 N_1(k)(t - k)
\end{aligned}$$

we can use the laws of logs to rewrite the LHS and take out a factor of $(t - k)$ on the RHS to obtain

$$\ln \left(\frac{N_1(t)}{N_1(k)} \right) = \left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} - d_1 N_1(k) \right) (t - k).$$

Taking exponentials of both sides yields

$$\frac{N_1(t)}{N_1(k)} = e^{\left(\left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} - d_1 N_1(k) \right) (t - k) \right)}$$

we can now multiply both sides by $N_1(k)$ to give us

$$N_1(t) = N_1(k) e^{\left(\left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} - d_1 N_1(k) \right) (t - k) \right)}.$$

By letting $t \rightarrow k + 1$, we obtain the discrete analogue of (3.11a) - (3.11b):

$$N_1(k + 1) = N_1(k) e^{\left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k)} - d_1 N_1(k) \right)} \quad (6.2a)$$

$$N_2(k + 1) = N_2(k) e^{\left(r_2 - \frac{b_2 N_2(k)}{1 + \alpha_{21} N_1(k)} - d_2 N_2(k) \right)}. \quad (6.2b)$$

We can also show, very similarly, that we can construct a discrete model with delays in the effect of mutualistic reactions represented as follows

$$N_1(k + 1) = N_1(k) e^{\left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k - \tau_2)} - d_1 N_1(k) \right)} = f_4(N_1, N_2) \quad (6.3a)$$

$$N_2(k + 1) = N_2(k) e^{\left(r_2 - \frac{b_2 N_2(k)}{1 + \alpha_{21} N_1(k - \tau_1)} - d_2 N_2(k) \right)} = g_4(N_1, N_2). \quad (6.3b)$$

The discrete systems also possess a nontrivial equilibrium point and this point coincides with that of the continuous model from which they are derived. So, by setting $N_1(k+1) = N_1(k) = N_1^*$ in (6.3a), and ignoring any points where one or more species are extinct,

$$N_1(k+1) = N_1(k)e^{\left(r_1 - \frac{b_1 N_1(k)}{1 + \alpha_{12} N_2(k-\tau_2)} - d_1 N_1(k)\right)}$$

gives

$$\begin{aligned} N_1^* &= N_1^* e^{\left(r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^*\right)} \\ \Rightarrow 1 &= e^{\left(r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^*\right)} \end{aligned}$$

we can take natural logs of both sides to obtain

$$\begin{aligned} \ln(1) &= r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^* \\ \Rightarrow 0 &= r_1 - N_1^* \left(\frac{b_1}{1 + \alpha_{12} N_2^*} + d_1 \right) \\ r_1 &= N_1^* \left(\frac{b_1 + d_1(1 + \alpha_{12} N_2^*)}{1 + \alpha_{12} N_2^*} \right) \\ \therefore N_1^* &= \frac{r_1(1 + \alpha_{12} N_2^*)}{b_1 + d_1(1 + \alpha_{12} N_2^*)}. \end{aligned}$$

Again we can similarly show that by setting $N_2(k+1) = N_2(k) = N_2^*$ in the (6.3b), we can find N_2^* and obtain our equilibrium point for the discrete model;

$$E = (N_1^*, N_2^*) = \left(\frac{r_1(1 + \alpha_{12} N_2^*)}{b_1 + d_1(1 + \alpha_{12} N_2^*)}, \frac{r_2(1 + \alpha_{21} N_1^*)}{b_2 + d_2(1 + \alpha_{21} N_1^*)} \right). \quad (6.4)$$

Now, let's evaluate the Jacobian for the delay model at this point. Next, consider (6.3a)

$$f_4(N_1, N_2) = N_1 e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)}$$

Using the product rule

$$\frac{\partial f_4(N_1, N_2)}{\partial N_1} = N_1 \times \frac{\partial}{\partial N_1} \left(e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)} \right) + \frac{\partial}{\partial N_1} (N_1) \times e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)}$$

Using the chain rule for the first term

$$\frac{\partial f_4(N_1, N_2)}{\partial N_1} = -N_1 \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2)}{1 + \alpha_{12}N_2} \right) \left(e^{r_1 - N_1 \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2)}{1 + \alpha_{12}N_2} \right)} \right) + e^{r_1 - N_1 \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2)}{1 + \alpha_{12}N_2} \right)}$$

Substituting in our value for N_1^*

$$\begin{aligned} \therefore \frac{\partial f_4(N_1^*, N_2^*)}{\partial N_1} &= - \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)} \right) \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right) \times \\ &\quad \left(e^{r_1 - \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)} \right) \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right)} \right) \\ &\quad + e^{r_1 - \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)} \right) \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right)} \end{aligned}$$

which cancels down to

$$\begin{aligned} \frac{\partial f_4(N_1^*, N_2^*)}{\partial N_1} &= -r_1 e^{r_1 - r_1} + e^{r_1 - r_1} \\ &= -r_1 e^0 + e^0 \\ &= -r_1 + 1 \\ &= 1 - r_1, \end{aligned}$$

similarly, we can show that

$$\frac{\partial g_4(N_1^*, N_2^*)}{\partial N_2} = 1 - r_2.$$

Next, we compute the remaining two elements of J

$$f_4(N_1, N_2) = N_1 e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right)}$$

using the chain rule

$$\begin{aligned}
\frac{\partial f_4(N_1, N_2)}{\partial N_2} &= N_1 e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)} \left(-b_1 N_1 \times \frac{\partial}{\partial N_2} \left(\frac{1}{1 + \alpha_{12} N_2 (k - \tau_2)} \right) \right) \\
&= N_1 e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)} \left(-b_1 N_1 \times \frac{\partial}{\partial N_2} \left(1 + \alpha_{12} N_2 (k - \tau_2) \right)^{-1} \right) \\
&= b_1 N_1^2 e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)} (1 + \alpha_{12} N_2 (k - \tau_2))^{-2} \alpha_{12} \times \frac{\partial}{\partial N_2} (N_2 (k - \tau_2)) \\
&= \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2 (k - \tau_2))^2} e^{\left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1\right)} \times \frac{\partial}{\partial N_2} (N_2 (k - \tau_2)) \\
&= \frac{\alpha_{12} b_1 N_1^2}{(1 + \alpha_{12} N_2 (k - \tau_2))^2} e^{\left(r_1 - N_1 \frac{b_1 + d_1 (1 + \alpha_{12} N_2)}{1 + \alpha_{12} N_2}\right)} \lambda^{-\tau_2},
\end{aligned}$$

hence

$$\frac{\partial f_4(N_1^*, N_2^*)}{\partial N_2} = \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^{\left(r_1 - \left(\frac{r_1 (1 + \alpha_{12} N_2^*)}{b_1 + d_1 (1 + \alpha_{12} N_2^*)} \right) \left(\frac{b_1 + d_1 (1 + \alpha_{12} N_2^*)}{1 + \alpha_{12} N_2^*} \right) \right)} \lambda^{-\tau_2}$$

the exponential term cancels down to

$$\begin{aligned}
\frac{\partial f_4(N_1^*, N_2^*)}{\partial N_2} &= \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^{(r_1 - r_1)} \lambda^{-\tau_2} \\
&= \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} e^0 \lambda^{-\tau_2}
\end{aligned}$$

therefore

$$\frac{\partial f_4(N_1^*, N_2^*)}{\partial N_2} = \frac{\alpha_{12} b_1 (N_1^*)^2}{(1 + \alpha_{12} N_2^*)^2} \lambda^{-\tau_2}.$$

We can show in the same manner that the final element is

$$\frac{\partial g_4(N_1^*, N_2^*)}{\partial N_1} = \frac{\alpha_{21} b_2 (N_2^*)^2}{(1 + \alpha_{21} N_1^*)^2} \lambda^{-\tau_1},$$

thus our Jacobian matrix looks like

$$J_E = \begin{pmatrix} 1 - r_1 & \frac{\alpha_{12}b_1(N_1^*)^2}{(1+\alpha_{12}N_2^*)^2}\lambda^{-\tau_2} \\ \frac{\alpha_{21}b_2(N_2^*)^2}{(1+\alpha_{21}N_1^*)^2}\lambda^{-\tau_1} & 1 - r_2 \end{pmatrix}. \quad (6.5)$$

Before we state our characteristic equation for this matrix, let's introduce some new ideas.

6.2.1 Preliminary

The following preliminary is from the work done by Elaydi [7]

Consider the k th order equation

$$x(n+k) + p_1x(n+k-1) + p_2x(n+k-2) + \cdots + P_kx(n) = 0 \quad (6.6)$$

where the p_i 's are real numbers.

The zero solution of equation (6.6) is asymptotically stable if and only if $|\lambda| < 1$ for every characteristic root λ of equation (6.6), that is for every zero of the characteristic polynomial

$$p(\lambda) = \lambda^k + p_1\lambda^{k-1} + \cdots + p_k. \quad (6.7)$$

We present the Schur-Cohn criterion which defines the conditions for the characteristic roots of equation (6.6) to fall inside the unit circle. Hence, this criterion is also a criterion for asymptotic stability.

Definition 5 (Inners of a matrix A). The inners of a square matrix A are the matrix itself and all the other matrices obtained by omitting successively the first and last rows and the first and last columns. For example, the inners for the following matrices are highlighted

$$A_{3 \times 3} = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & \boxed{a_{22}} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

$$A_{4 \times 4} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & \boxed{a_{22} \quad a_{23}} & a_{24} \\ a_{31} & \boxed{a_{32} \quad a_{33}} & a_{34} \\ a_{41} & a_{42} & a_{43} & a_{44} \end{pmatrix}$$

$$A_{5 \times 5} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} \\ a_{21} & \boxed{a_{22} \quad a_{23} \quad a_{24}} & a_{25} \\ a_{31} & \boxed{a_{32} \quad \boxed{a_{33}} \quad a_{34}} & a_{35} \\ a_{41} & \boxed{a_{42} \quad a_{43} \quad a_{44}} & a_{45} \\ a_{51} & a_{52} & a_{53} & a_{54} & a_{55} \end{pmatrix}$$

Definition 6 (Positive Innerwise). A matrix A is said to be *positive innerwise* if the determinants of all of its inners are positive.

Theorem 6.1 (Shur-Cohn criterion). The zeros of the characteristic polynomial (6.7) lie inside the unit circle if and only if the following hold:

1. $p(1) > 0$,
2. $(-1)^k p(-1) > 0$,
3. the $(k-1) \times (k-1)$ matrices

$$A_{k-1}^{\pm} = \begin{pmatrix} 1 & 0 & \cdots & 0 \\ p_1 & 1 & \cdots & 0 \\ \vdots & & & \vdots \\ p_{k-3} & & & \\ p_{k-2} & p_{k-3} & \cdots & p_1 & 1 \end{pmatrix} \pm \begin{pmatrix} 0 & 0 & \cdots & p_k \\ 0 & 0 & \cdots & p_k & p_{k-1} \\ \vdots & \vdots & & \vdots \\ 0 & p_k & & p_3 \\ p_k & p_{k-1} & \cdots & p_3 & p_2 \end{pmatrix}$$

are positive innerwise.

Example 6.1. Consider the equation

$$x(n+2) + p_1 x(n+1) + p_2 x(n) = 0 \quad (6.8)$$

Its characteristic polynomial is given by

$$p(\lambda) = \lambda^2 + p_1 \lambda + p_2.$$

Let us attempt to discover the conditions which make the zero solution of equation (6.8) asymptotically stable. Using the Schur-Cohn criterion (see Theorem 6.1), we require

$$p(1) = 1 + p_1 + p_2 > 0$$

and

$$p(-1) = 1 - p_1 + p_2 > 0.$$

This implies that $1 + p_2$. From condition 3 we stipulate that $1 - p_2 > 0$ or $p_2 < 1$.

Thus a necessary and sufficient condition for the zero solution of equation (6.8) to be asymptotically stable is

1. $1 + p_1 + p_2 > 0$,
2. $1 - p_1 + p_2 > 0$,
3. $p_2 < 1$.

See [7].

We shall use this information when determining the stability of our discrete model of mutualism. We notice that the Jacobian matrix (6.5) leads to a characteristic polynomial of the form

$$\lambda^{\tau+2} - Q\lambda^{\tau+1} + R\lambda^{\tau} - S = 0 \quad (6.9)$$

where

$$\begin{aligned} Q &= 2 - (r_1 + r_2), \\ R &= (1 - r_1)(1 - r_2), \\ S &= \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}\lambda^{-\tau}, \\ \tau &= \tau_1 + \tau_2. \end{aligned}$$

We focus on the special case, $\tau_1 = \tau_2 = 0$ of our derived model and show that this model corresponds to a different stability region to that of (3.11a) - (3.11b). For the non-delay case, our characteristic equation becomes

$$\lambda^{0+2} - Q\lambda^{0+1} + R\lambda^0 - S = 0$$

which can be more simply written as

$$\lambda^2 - Q\lambda + R - S = 0$$

where

$$Q = 2 - (r_1 + r_2),$$

and

$$R - S = (1 - r_1)(1 - r_2) - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}.$$

We notice that $Q = 2 - (r_1 + r_2)$ is equal to the trace¹ of J . We also notice that the determinant of J is equal to $R - S$. So, with this information at hand we can re-write our characteristic polynomial as a quadratic in the form

$$\lambda^2 - \text{Tr}(J)\lambda + \det(J) = 0 \tag{6.10}$$

where

$$\text{Tr}(J) = 2 - (r_1 + r_2),$$

and

$$\det(J) = (1 - r_1)(1 - r_2) - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}.$$

We can now prove the following result:

¹The trace of an $n \times n$ square matrix A is the sum of the leading diagonal elements of A i.e. $\text{Tr}(A) = \sum_{i=1}^n a_{ii}$

Theorem 6.2. Assume that $r_1, r_2, b_1, b_2, d_1, d_2 \in (0, \infty)$, $\alpha_{12}, \alpha_{21} \in [1, \infty)$. Then the positive steady state $E = (N_1^*, N_2^*)$ of the discrete system (6.2a) - (6.2b) with initial conditions $N_1(0) > 0$, $N_2(0)$ is asymptotically stable providing that

$$2 + \frac{\Phi}{2} > (r_1 + r_2) > \Phi \quad (6.11)$$

where

$$\Phi = r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2}.$$

Proof. It is stated (see preliminary section earlier) that, for asymptotic stability of a second order system we require the following conditions to hold

1. $1 + \text{Tr}(J) + \det(J) > 0$,
2. $1 - \text{Tr}(J) + \det(J) > 0$,
3. $\det(J) < 1$.

Let's prove the first condition. Using our identities for $\text{Tr}(J)$ and $\det(J)$ we get

$$\begin{aligned} 1 + \text{Tr}(J) + \det(J) &= 1 + 2 - (r_1 + r_2) + (1 - r_1)(1 - r_2) - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \\ &= 1 + 2 - r_1 - r_2 + 1 - r_1 - r_2 + r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \\ &= 4 - 2(r_1 + r_2) + \Phi \end{aligned}$$

with Φ as stated in the theorem. Let's assume that this is greater than zero, we get

$$4 - 2(r_1 + r_2) + \Phi > 0.$$

Dividing both sides by 2 yields

$$2 - (r_1 + r_2) + \frac{\Phi}{2} > 0$$

which can be rearranged to

$$2 + \frac{\Phi}{2} > (r_1 + r_2)$$

which we know is true from (6.11). Hence, the first condition holds.

For the second condition, using our identities for $\text{Tr}(J)$ and $\det(J)$ we have

$$\begin{aligned}
1 - \text{Tr}(J) + \det(J) &= 1 - [2 - (r_1 + r_2)] + (1 - r_1)(1 - r_2) - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \\
&= 1 - 2 + r_1 + r_2 + 1 - r_1 - r_2 + r_1r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}, \\
&= r_1r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}
\end{aligned}$$

by lemma (5.1) we know that

$$r_1r_2 > \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2}$$

hence it is clear to see that

$$r_1r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} > 0$$

is true, thus proving our second condition.

Finally we shall prove our third condition. Using our identity for $\det(J)$, consider

$$\begin{aligned}
1 - \det(J) &= 1 - \left((1 - r_1)(1 - r_2) - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \right) \\
&= 1 - (1 - r_1)(1 - r_2) + \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \\
&= 1 - (1 - r_1 - r_2 + r_1r_2) + \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \\
&= r_1 + r_2 - r_1r_2 + \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \\
&= r_1 + r_2 - \left(r_1r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \right) \\
&= r_1 + r_2 - \Phi
\end{aligned}$$

by (6.11), we know that

$$r_1 + r_2 > \Phi$$

therefore, it is clear to see that

$$r_1 + r_2 - \bar{\Phi} > 0$$

hence

$$1 - \det(J) > 0$$

i.e.

$$\det(J) < 1.$$

So our third and final condition holds, thus proving the theorem and confirming asymptotic stability for the system (6.2a) - (6.2b).

□

6.3 Numerical Methods

6.3.1 Introduction to Numerical Methods

It is very often not possible to solve differential equations analytically, take the following initial-value problem for instance

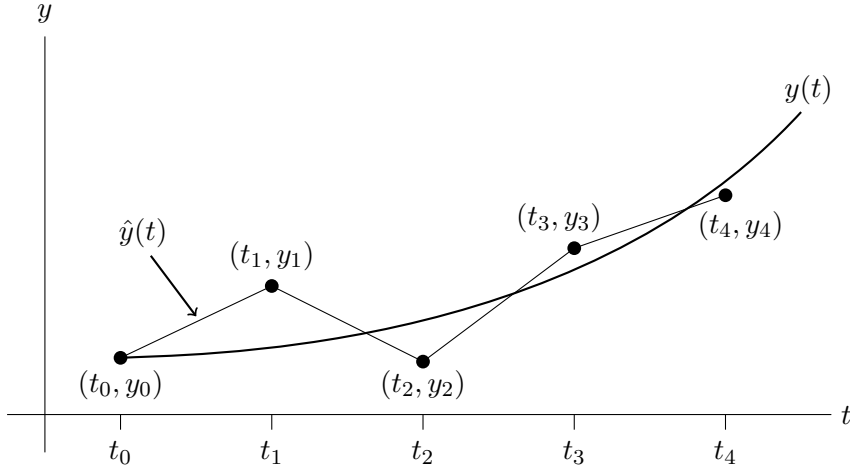
$$y'(t) = f(t, y), \quad y(t_0) = y_0. \quad (6.12)$$

Therefore, in order for such differential equations to have any practical use to us, we must devise ways of obtaining accurate approximations of the solution $y(t)$ of (6.12). Now, there's no way we could approximate a function on an entire interval $t_0 \leq t \leq t_0 + a$ since this would require an infinite amount of information. However, what we can do is approximate values y_1, y_2, \dots, y_N of $y(t)$ at a finite number of points t_1, t_2, \dots, t_N to obtain an approximation of $y(t)$ on the entire interval $t_0 \leq t \leq t_0 + a$ [4].

6.3.2 Euler's Scheme

The following construction of Euler's scheme is heavily based on a similar construction taken from Braun [4]. Let $\hat{y}(t)$ be the function whose graph on each interval $[t_i, t_{i+1}]$ is the straight line connecting the points (t_i, y_i) and (t_{i+1}, y_{i+1}) (see Figure 6.2), we can express $\hat{y}(t)$ analytically by the equation

$$\hat{y}(t) = y_i + \frac{1}{h}(t - t_i)(y_{i+1} - y_i), \quad t_i \leq t \leq t_{i+1}.$$

Figure 6.2: Graph showing the comparison between $\hat{y}(t)$ and $y(t)$

If $\hat{y}(t)$ is close to $y(t)$ at $t = t_i$; that is, if y_i is close to $y(t_i)$, and if t_{i+1} is close to t_i , then $\hat{y}(t)$ is close to $y(t)$ on the entire interval $t_i \leq t \leq t_{i+1}$. This follows immediately from the continuity of both $y(t)$ and $\hat{y}(t)$. Thus, we need only devise schemes for obtaining accurate approximations of $y(t)$ at a discrete number of points t_1, t_2, \dots, t_N in the interval $t_0 \leq t \leq t_0 + a$. For simplicity, we will require the points t_1, t_2, \dots, t_N to be equally spaced. This is achieved by choosing a large $N \in \mathbb{Z}$ and setting $t_n = t_0 + k \left(\frac{a}{N}\right)$, $n = 1, 2, \dots, N$. Alternatively, we may write $t_{n+1} = t_n + h$ where $h = \frac{a}{N}$.

Now, the only thing we know about $y(t)$ is that it satisfies a certain differential equation (i.e. (6.12)), and that its value at $t = t_0$ is y_0 . We shall use this information to approximate a value for y_1 of y at $t = t_1 = t_0 + h$. Then, we will use the approximation y_1 to find an approximate value for y_2 of y at $t = t_2 = t_1 + h$ and so on. In order to accomplish this we must use a theorem which enables us to compute the value of y at $t = t_n + h$ from the knowledge of y at $t = t_n$. The theorem we shall use, is Taylor's Theorem,

$$y(t_n + h) = y(t_n) + h \frac{dy(t_n)}{dt} + \frac{h^2}{2!} \frac{d^2 y(t_n)}{dt^2} + \dots \quad (6.13)$$

Thus, if we know the value of y and its derivatives at $t = t_n$, then we can compute the value of y at $t = t_n + h$. Now, $y(t)$ satisfies the initial-value problem (6.12). Hence, its derivative, when evaluated at $t = t_n$, must equal $f(t_n, y(t_n))$. Moreover, by repeated use of the chain rule of partial differentiation (see Appendix A), we can evaluate

$$\frac{d^2 y(t_n)}{dt^2} = \left[\frac{\partial f}{\partial t} + f \frac{\partial f}{\partial y} \right] (t_n, y(t_n))$$

and all other higher-order derivatives of $y(t)$ at $t = t_n$. Hence, we can rewrite (6.13) as an equation in the form

$$y(t_n + h) = y(t_n) + h f(t_n, y(t_n)) + \frac{h^2}{2!} \left[\frac{\partial f}{\partial t} + f \frac{\partial f}{\partial y} \right] (t_n, y(t_n)) + \dots \quad (6.14)$$

The simplest approximation of $y(t_{n+1})$ is obtained by truncating the Taylor series (6.14) after the second term. This gives rise to the numerical scheme

$$y_1 = y_0 + h f(t_0, y_0), \quad y_2 = y_1 + h f(t_1, y_1),$$

and, in general

$$y_{n+1} = y_n + hf(t_n, y_n), \quad y_0 = y(t_0). \quad (6.15)$$

Notice how we use the initial-value y_0 and the fact that $y(t)$ satisfies the differential equation $y'(t) = f(t, y)$ to compute an approximation y_1 of $y(t)$ at $t = t_1$. Then, we use y_1 to approximate y_2 at $t = t_2$, and so on.

Equation (6.15) is known as Euler's scheme [4].

6.4 Discretising the model (3.11a) - (3.11b) through application of Euler's Scheme

Applying Euler's scheme to our earlier system

$$\begin{aligned} \frac{dN_1}{dt} &= \left(r_1 - \frac{b_1 N_1}{1 + \alpha_{12} N_2} - d_1 N_1 \right) N_1 \\ \frac{dN_2}{dt} &= \left(r_2 - \frac{b_2 N_2}{1 + \alpha_{21} N_1} - d_2 N_2 \right) N_2 \end{aligned}$$

yields the following discrete system

$$N_1(t_{n+1}) = N_1(t_n) + hN_1(t_n) \left(r_1 - \frac{b_1 N_1(t_n)}{1 + \alpha_{12} N_2(t_n)} - d_1 N_1(t_n) \right) \quad (6.16a)$$

$$N_2(t_{n+1}) = N_2(t_n) + hN_2(t_n) \left(r_2 - \frac{b_2 N_2(t_n)}{1 + \alpha_{21} N_1(t_n)} - d_2 N_2(t_n) \right). \quad (6.16b)$$

Let's find the nontrivial equilibrium points in a similar manner as before. Setting $N_1(t_{n+1}) = N_1(t_n) = N_1^*$, equation (6.16a) becomes

$$\begin{aligned} N_1^* &= N_1^* + hN_1^* \left(r_1 - \frac{b_1 N_1^*}{1 + \alpha_{12} N_2^*} - d_1 N_1^* \right) \\ \Rightarrow 0 &= hr_1 N_1^* - \frac{hb_1 (N_1^*)^2}{1 + \alpha_{12} N_2^*} - hd_1 (N_1^*)^2 \end{aligned}$$

dividing both sides by N_1^* gives us

$$0 = hr_1 - \frac{hb_1 N_1^*}{1 + \alpha_{12} N_2^*} - hd_1 N_1^*$$

which can be rearranged to obtain

$$hr_1 = \frac{hb_1 N_1^*}{1 + \alpha_{12} N_2^*} + hd_1 N_1^*.$$

Taking out a factor of N_1^* on the RHS yields

$$hr_1 = N_1^* \left(\frac{hb_1}{1 + \alpha_{12}N_2^*} + hd_1 \right),$$

we can find a common denominator on the RHS to obtain a single fraction

$$hr_1 = N_1^* \left(\frac{hb_1 + hd_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right)$$

and solving for N_1^* ;

$$N_1^* = \frac{hr_1(1 + \alpha_{12}N_2^*)}{h(b_1 + d_1(1 + \alpha_{12}N_2^*))}$$

the h 's cancel on the RHS and we arrive at

$$N_1^* = \frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)}$$

and we can find again that

$$N_2^* = \frac{r_2(1 + \alpha_{21}N_1^*)}{b_2 + d_2(1 + \alpha_{21}N_1^*)}$$

giving us our non-trivial equilibrium point

$$E = (N_1^*, N_2^*) = \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)}, \frac{r_2(1 + \alpha_{21}N_1^*)}{b_2 + d_2(1 + \alpha_{21}N_1^*)} \right)$$

for the system. We notice that it corresponds to those found before. We can now find the partial derivatives required to construct our next Jacobian matrix. Let

$$N_1(t_{n+1}) = N_1(t_n) + hN_1(t_n) \left(r_1 - \frac{b_1N_1(t_n)}{1 + \alpha_{12}N_2(t_n)} - d_1N_1(t_n) \right) = f_5$$

$$N_2(t_{n+1}) = N_2(t_n) + hN_2(t_n) \left(r_2 - \frac{b_2N_2(t_n)}{1 + \alpha_{21}N_1(t_n)} - d_2N_2(t_n) \right) = g_5$$

consider f_5

$$f_5 = N_1 + hN_1 \left(r_1 - \frac{b_1N_1}{1 + \alpha_{12}N_2} - d_1N_1 \right)$$

expanding brackets gives us

$$f_5 = N_1 + hN_1r_1 - \frac{hb_1N_1^2}{1 + \alpha_{12}N_2} - hd_1N_1^2$$

differentiating f_5 with respect to N_1 yields

$$\begin{aligned}\frac{\partial f_5}{\partial N_1} &= 1 + hr_1 - 2\frac{hb_1N_1}{1 + \alpha_{12}N_2} - 2hd_1N_1 \\ &= 1 + hr_1 - 2hN_1 \left(\frac{b_1}{1 + \alpha_{12}N_2} + d_1 \right) \\ &= 1 + hr_1 - 2hN_1 \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2)}{1 + \alpha_{12}N_2} \right)\end{aligned}$$

the partial derivative at our equilibrium point is therefore

$$\frac{\partial f_5(N_1^*, N_2^*)}{\partial N_1} = 1 + hr_1 - 2hN_1^* \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right).$$

Substituting our value for N_1^* into the RHS gives us

$$\frac{\partial f_5(N_1^*, N_2^*)}{\partial N_1} = 1 + hr_1 - 2h \left(\frac{r_1(1 + \alpha_{12}N_2^*)}{b_1 + d_1(1 + \alpha_{12}N_2^*)} \right) \left(\frac{b_1 + d_1(1 + \alpha_{12}N_2^*)}{1 + \alpha_{12}N_2^*} \right)$$

which simplifies down to

$$\begin{aligned}\frac{\partial f_5(N_1^*, N_2^*)}{\partial N_1} &= 1 + hr_1 - 2hr_1 \\ &= 1 - hr_1.\end{aligned}$$

Again, we can similarly show that

$$\frac{\partial g_5(N_1^*, N_2^*)}{\partial N_2} = 1 - hr_2.$$

Next, we have

$$f_5 = N_1 + hN_1r_1 - \frac{hb_1N_1^2}{1 + \alpha_{12}N_2} - hd_1N_1^2$$

differentiating with respect to N_2 gives us

$$\frac{\partial f_5}{\partial N_2} = -\frac{hb_1N_1^2}{1 + \alpha_{12}N_2}$$

use of the chain rule yields

$$\frac{\partial f_5}{\partial N_2} = -hb_1 N_1^2 \left(\frac{-\alpha_{12}}{(1 + \alpha_{12} N_2)^2} \right)$$

the partial derivative at our equilibrium point is therefore

$$\frac{\partial f_5(N_1^*, N_2^*)}{\partial N_2} = \frac{h\alpha_{12}b_1 (N_1^*)^2}{(1 + \alpha_{12}N_2^*)^2}.$$

Again, we know that we can show that also

$$\frac{\partial g_5(N_1^*, N_2^*)}{\partial N_1} = \frac{h\alpha_{21}b_2 (N_2^*)^2}{(1 + \alpha_{21}N_1^*)^2},$$

thus giving us our Jacobian matrix for our system

$$J_E = \begin{pmatrix} 1 - hr_1 & \frac{h\alpha_{12}b_1 (N_1^*)^2}{(1 + \alpha_{12}N_2^*)^2} \\ \frac{h\alpha_{21}b_2 (N_2^*)^2}{(1 + \alpha_{21}N_1^*)^2} & 1 - hr_2 \end{pmatrix}. \quad (6.17)$$

Next, we state our final result and give a proof.

Theorem 6.3. Assume that $r_1, r_2, b_1, b_2, d_1, d_2 \in (0, \infty)$, $\alpha_{12}, \alpha_{21} \in [1, \infty)$. Then the positive steady state $E = (N_1^*, N_2^*)$ of the discrete system (6.16a) - (6.16b) with initial conditions $N_1(0) > 0$, $N_2(0)$ is asymptotically stable in the limit as $h \rightarrow 0$.

Proof. We can find the characteristic equation of the Jacobian matrix (6.17) in the following manner

$$\begin{aligned} \det(J_E - \lambda I) &= 0 \\ \Rightarrow \det \begin{pmatrix} 1 - hr_1 - \lambda & \frac{h\alpha_{12}b_1 (N_1^*)^2}{(1 + \alpha_{12}N_2^*)^2} \\ \frac{h\alpha_{21}b_2 (N_2^*)^2}{(1 + \alpha_{21}N_1^*)^2} & 1 - hr_2 - \lambda \end{pmatrix} &= 0 \end{aligned}$$

which yields

$$(1 - hr_1 - \lambda)(1 - hr_2 - \lambda) - \left(\frac{h\alpha_{12}b_1 (N_1^*)^2}{(1 + \alpha_{12}N_2^*)^2} \right) \left(\frac{h\alpha_{21}b_2 (N_2^*)^2}{(1 + \alpha_{21}N_1^*)^2} \right) = 0$$

expanding brackets gives us

$$\lambda^2 - \lambda - \lambda - hr_1 - hr_2 + \lambda hr_1 + \lambda hr_2 + h^2 r_1 r_2 + 1 - \frac{h^2 \alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} = 0.$$

Further rearranging and factorisation occurs over the next two steps

$$\lambda^2 - 2\lambda - h(r_1 + r_2) + \lambda h(r_1 + r_2) + h^2 r_1 r_2 + 1 - \frac{h^2 \alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} = 0$$

$$\lambda^2 - \lambda(2 - h(r_1 + r_2)) + 1 - h(r_1 + r_2) + h^2 \left(r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2} \right) = 0.$$

We note again that the trace and the determinant of the Jacobian matrix (6.17) are

$$\text{Tr}(J) = 2 - h(r_1 + r_2)$$

$$\det(J) = 1 - h(r_1 + r_2) + h^2 \Phi$$

respectively, where

$$\Phi = r_1 r_2 - \frac{\alpha_{12} \alpha_{21} b_1 b_2 (N_1^* N_2^*)^2}{(1 + \alpha_{12} N_2^*)^2 (1 + \alpha_{21} N_1^*)^2}.$$

We therefore notice that the characteristic equation can be rewritten as

$$\lambda^2 - \text{Tr}(J) + \det(J) = 0. \tag{6.18}$$

In order to determine asymptotic stability in the limit as $h \rightarrow 0$, we again need to show that the following conditions hold;

1. $1 + \text{Tr}(J) + \det(J) > 0$,
2. $1 - \text{Tr}(J) + \det(J) > 0$,
3. $\det(J) < 1$.

Let's begin, this time, with the third condition,

$$\det(J) < 1$$

substituting our expression for $\det(J)$ gives us

$$1 - h(r_1 + r_2) + h^2 \Phi < 1$$

which simplifies down to

$$h^2 \Phi < h(r_1 + r_2).$$

Dividing both sides by h , we get

$$h\Phi < (r_1 + r_2)$$

which holds true since $\Phi > 0$ (from Lemma (5.1)), since we can only choose $r_1, r_2 \in (0, \infty)$ in the limit $h \rightarrow 0$. Next, let's prove the first condition,

$$1 + \text{Tr}(J) + \det(J) > 0$$

may be rewritten as

$$\begin{aligned} & 1 + 2 - h(r_1 + r_2) + 1 - h(r_1 + r_2) + h^2\Phi > 0 \\ \Rightarrow & 1 + 2 - h(r_1 + r_2) + 1 - h(r_1 + r_2) + h^2 \left(r_1 r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \right) > 0 \\ \Rightarrow & 4 - 2h(r_1 + r_2) + h^2r_1r_2 - h^2 \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} > 0 \end{aligned}$$

taking the limit as $h \rightarrow 0$ yields

$$\lim_{h \rightarrow 0} \left(4 - 2h(r_1 + r_2) + h^2r_1r_2 - h^2 \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \right) = 4$$

The first condition holds since $4 > 0$. Finally, for the second condition,

$$1 - \text{Tr}(J) + \det(J) > 0$$

may be rewritten as

$$\begin{aligned} & 1 - (2 - h(r_1 + r_2)) + 1 - h(r_1 + r_2) + h^2 \left(r_1 r_2 - \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} \right) > 0 \\ \Rightarrow & 1 - 2 + h(r_1 + r_2) + 1 - h(r_1 + r_2) + h^2r_1r_2 - h^2 \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} > 0. \end{aligned}$$

Thus

$$\begin{aligned} & h^2r_1r_2 - h^2 \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} > 0 \\ \Rightarrow & h^2 \frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1 + \alpha_{12}N_2^*)^2(1 + \alpha_{21}N_1^*)^2} < h^2r_1r_2 \end{aligned}$$

dividing through by h^2 gives us

$$\frac{\alpha_{12}\alpha_{21}b_1b_2(N_1^*N_2^*)^2}{(1+\alpha_{12}N_2^*)^2(1+\alpha_{21}N_1^*)^2} < r_1r_2$$

which we know to be true from Lemma (5.1) thus proving our second condition. All three conditions are now proved to be true, this confirms asymptotic stability for the system (6.16a) - (6.16b). \square

6.5 Graphical Comparison of Discrete Models

There are a range of parameter values that exist for which the discrete model, derived using the methodology of piecewise constant arguments does not possess an asymptotically stable equilibrium in the positive quadrant. We must be very careful when using this approach when creating discrete models: the underlying stability properties do not transfer across so readily [32].

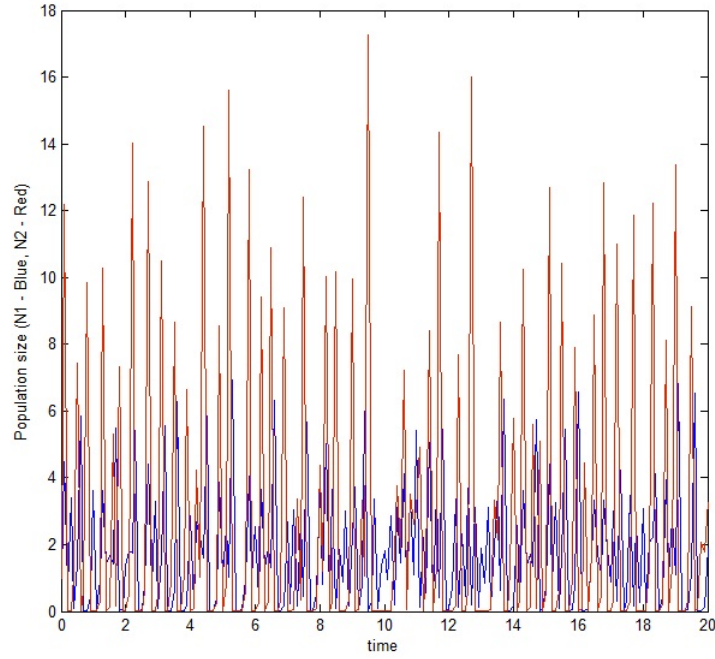


Figure 6.3: Graph showing the piecewise discrete model (6.2a) - (6.2b) with parameter values $\alpha_{12} = \alpha_{21} = b_1 = b_2 = d_1 = d_2 = 1$, $r_1 = 3$, $r_2 = 4$ and a step size $h = 0.1$

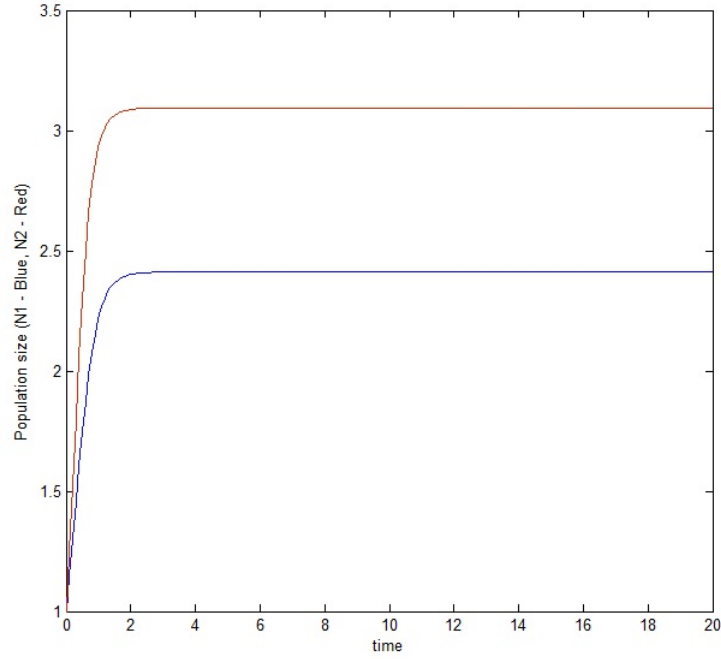


Figure 6.4: Graph showing the Euler scheme model (6.16a) - (6.16b) with parameter values $\alpha_{12} = \alpha_{21} = b_1 = b_2 = d_1 = d_2 = 1$, $r_1 = 3$, $r_2 = 4$ and a step size $h = 0.1$

The above graphs illustrate, quite clearly, the differences between the two models when the same parameter values are used. Figure 6.3 shows persistent oscillatory behaviour from both species for the discrete model (6.3a) - (6.3b). Figure 6.4 shows clear asymptotic stability from both species as they plateau, as we would expect, species 2 reaches a higher plateau since $r_2 > r_1$. Despite the fact that all parameter values are the same, as is the step size of both methods used on exactly the same model (3.11a)-(3.11b) (in fact, only the methods themselves are different), we see dramatically different results.

Chapter 7

Conclusion

7.1 What have we found?

We have found that simply changing the signs of a simple competition model to create a positive interaction yields unrealistic long term population behaviour. We have found that the improved models we have constructed are asymptotically stable at their non-trivial equilibrium point for the non-delay ODE and the DDE. Our discrete models are also asymptotically stable although we have found that when discretising our model, it is important to do so with caution as different techniques can yield substantially different behaviour over time. We see in chapter 6 that using piecewise constant arguments yields tremendously different results than when the Euler scheme is implemented. We note that our model (3.11a)-(3.11b) may not be applicable to every real world situation, there may indeed be situations where behaviour from figure 6.3 is displayed and other situations where behaviour from figure 6.4 is displayed.

7.2 Future work

When considering further work to undertake beyond this dissertation, we must contemplate where the area of mutualism within population dynamics is heading with regard to the world of mathematics. Now, this field of study is remarkably vast, hence there are many directions in which the research we have done may head.

Alternative numerical schemes

We can create even more accurate models by applying more complicated numerical schemes instead of our Euler one, such schemes may include the improved-Euler scheme, Runge-Kutta and the Newton-Raphson methods. Care should be taken though since application of more complicated schemes will undoubtedly create very difficult difference equations and problems in computing such schemes may arise on MATLAB etc.

Stochastic models

We can make our models more complicated and thus more realistic through a number of ways, one of which could be to note that we have featured fixed constants in our systems throughout this dissertation. The constants b_1, b_2 , for example denote the birth rate for species 1 and species 2 respectively, however, it is very naive to assume that the birth rate is a constant as it is much more likely to be a function. Let's assume that all of our

constants are now functions of time, the system (3.11a)-(3.11b) now takes the following form;

$$\begin{aligned}\frac{dN_1(t)}{dt} &= \left(r_1(t) - \frac{b_1(t)N_1(t)}{1 + \alpha_{12}(t)N_2(t)} - d_1(t)N_1(t) \right) N_1(t) \\ \frac{dN_2(t)}{dt} &= \left(r_2(t) - \frac{b_2(t)N_2(t)}{1 + \alpha_{21}(t)N_1(t)} - d_2(t)N_2(t) \right) N_2(t).\end{aligned}$$

Occurrences such as death, for example, may not always be subject to time. Especially in nature, death is something that can happen at any time from many different factors. In fact, population systems in reality are often subject to environmental noise making it even more difficult for mathematicians to entertain the idea of having parameters as absolute constants. As a result of this, the field of study has seen the rise of stochastic population systems, Mao *et al* [24] put across the conclusion that even a sufficiently small noise can suppress explosions in population dynamics. Qiu *et al* [30] also looks into this by taking the following mutualism model originally proposed by Gopalsamy; [11]

$$\frac{dN_1(t)}{dt} = r_1(t)N_1(t) \left(\frac{K_1(t) + \alpha_1(t)N_2(t)}{1 + N_2(t)} - N_2(t) \right) \quad (7.2a)$$

$$\frac{dN_2(t)}{dt} = r_2(t)N_2(t) \left(\frac{K_2(t) + \alpha_2(t)N_1(t)}{1 + N_1(t)} - N_1(t) \right), \quad (7.2b)$$

transforming (7.2a)-(7.2b) into the system of the following form

$$\frac{dx(t)}{dt} = x(t) \left(\frac{a_1(t) + a_2(t)y(t)}{1 + y(t)} - c_1(t)x(t) \right) \quad (7.3a)$$

$$\frac{dy(t)}{dt} = y(t) \left(\frac{b_1(t) + b_2(t)x(t)}{1 + x(t)} - c_2(t)y(t) \right) \quad (7.3b)$$

and by taking into account the effects of a randomly fluctuating environment, they incorporate white noise in each equation of the system (7.3a) - (7.3b). Therefore the non-autonomous stochastic system can be described by the following Itô equation

$$dx(t) = x(t) \left(\frac{a_1(t) + a_2(t)y(t)}{1 + y(t)} - c_1(t)x(t) \right) dt + \sigma_1(t)x(t)dB_1(t) \quad (7.4a)$$

$$dy(t) = y(t) \left(\frac{b_1(t) + b_2(t)x(t)}{1 + x(t)} - c_2(t)y(t) \right) dt + \sigma_2(t)y(t)dB_2(t) \quad (7.4b)$$

where $a_i(t)$, $b_i(t)$, $c_i(t)$, σ_i , $i = 1, 2$ are all positive, continuous and bounded functions on $[0, +\infty)$ and $B_1(t), B_2(t)$ are independent Brownian motions and σ_1, σ_2 represent the intensities of white noise. The paper goes on to consider dynamical properties of the stochastic system (7.4a) - (7.4b). For future work, we would look to study this further and use similar techniques in order to introduce stochasticity to our models.

Data Collection

One important aspect of mathematical modelling that has eluded us here is the ability to verify the models through collection of data, an aim for our future work would be to

do this. An example of data collection in population modelling can be found in the book by Braun [4] in which we can find an equation for population as a function of time. The model is used to predict the population of the U.S. from the years 1790-1950 at seventeen intervals, this is then compared with the actual data. This could be extended to population numbers of insects and plants for example.

Considering the specificity of the mutualism

The 'specificity' of the mutualism interaction is a way of classifying the mutualism in terms of the number of species involved, we have the terms *specialised* mutualism which involves a one-to-one interaction and *diffuse* mutualism which involves many species. So far, we have only considered specialised mutualism models, but of course in the reality of nature there is very rarely only ever two species in any given space. Suppose that we consider a model for diffuse mutualism that involves $n > 2$ species, could it be that all species benefit each other's existence? If this is the case, then what would happen to the model? Well, firstly we would need n equations representing the growth rate (with respect to time) of each species whose populations shall be denoted as before, i.e. N_1, N_2, \dots, N_n . We would also have $(n - 1) \times \alpha_{ij}$ parameters representing the strength of the mutualistic effects of species j on species i , where $i = 1, 2, \dots, n$, $j = 1, 2, \dots, n$, $i \neq j$ within each of our n equations. Each equations shall also include b_n, d_n, r_n terms as before, e.g.

$$\begin{aligned} \frac{dN_1}{dt} &= f_1(N_1, N_2, \dots, N_n) \\ \frac{dN_2}{dt} &= f_2(N_1, N_2, \dots, N_n) \\ &\vdots \\ \frac{dN_n}{dt} &= f_n(N_1, N_2, \dots, N_n) \end{aligned}$$

where f_i , $i = 1, \dots, n$ represents a function of all n species. Such a model would of course be very difficult to be investigated and its behaviour would prove even more difficult since phase portraits would only be available through graphical representation at a maximum of three species in a 3D graph.

Vicinity dependent models

An interesting assumption is being made when modelling this subject matter. We assume that vicinity has no impact on our models; that mutualists are readily available for the species we are modelling. Now, this makes sense due to the fact that if two species help each other thrive then they should naturally tend towards each other. However, many species of animals do not travel individually, they travel in groups. An intriguing suggestion for further work would be that modelling certain species that we assume to exist in 'herds', and that their herd covers a certain area, would there be a point at which mutualism between two species can reach an optimum should their respective 'herds' interact to form, in essence, a virtual Venn diagram? Would there be a certain area of the Venn diagram that would make the model unstable?

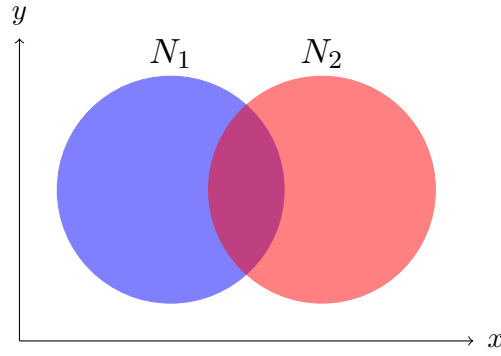


Figure 7.1: Visual representation of the idea of a vicinity based model in which the species 1 and 2 occupy the blue and red circles respectively and the mutualistic strength of the model is dependent of the area of the intersection (purple).

More parameters must be introduced to facilitate this idea. A two-dimensional plane (see figure 7.1) could be modelled with the mutualistic effects of each species being a function of both space and time e.g. $\alpha_{12}(x, y, t)$.

Spatial models

In reality, certain geographical locations may not be ideal for mutualism to occur at the best rate, constants within the models that we construct may be influenced as a result of the location in which the model is based. Also, in light of the idea of a vicinity dependent model, we realise that groups of organisms do not conveniently position themselves into uniform patterns. It has been found, however, that their distribution is not random either; in fact, they form some sort of spatial pattern. Natural environments are spatially structured by various ecological processes, which in combination with the behavioural response of the species, generally results in gradients (steady directional change in numbers over a specific distance), patches (a relatively uniform and homogenous area separated by gaps) and noise variation (random fluctuations) [35]. As interesting and idea as this is, it is also noteworthy that there are few models of this kind that exist due to nature rarely following an expected order, mostly observational data has been collected in this area as opposed to theoretical models. Spatially structured models look heavily into PDEs (partial differential equations).

	Continuous time	Discrete time
Continuous space	Reaction-diffusion equations	Integro-differential equations
Discrete space	Coupled-patch models Metapopulation models	Coupled lattice maps Cellular automata

Table 7.1: Table taken from Kot [16] displaying examples of spatially structured models as they differ between continuous and discrete time and continuous and discrete space.

The recent research letter [36] by Suweis *et al* looks at how an optimisation principle aimed at maximising the species abundance in mutualistic communities can give rise to the emergence of nested¹ interaction networks.

¹Nestedness is a measure of order in an ecological system, referring to the order in which the number of species is related to area or other factors. The more a system is "nested" the more it is organized [29].

Further evidence that the aspects of structure, nestedness and optimisation in the research area of mutualistic models is becoming more and more important can be found by Rohr *et al* [33] in which it is investigated to what extent different network architectures² of mutualistic systems can provide a wider range of conditions under which species can exist. It is noted in the article that framework of structural stability has not been as dominant in past research into theoretical ecology as has the concept of local stability. The article also highlights the need for a stochastic aspect in this field as they use a mean field approximation for the competition parameters in models that are used.

Diverting from mutualism

If we were to take a step aside from mutualism, and avoid the well-researched predator-prey models, there are numerous other symbiotic interactions that may be studied in depth. Notable interactions include;

Parasitism

Parasitism is where one species benefits at the expense of the other e.g. leeches suck blood from its host in order to survive.

Commensalism

Commensalism is an interaction that involves one species benefiting and the other receiving no effect e.g. trees provides homes for birds whilst receiving no beneficial return.

Amensalism

Amensalism is when the existence of one species has a detrimental effect on another but remains unaffected in return. An example of this includes the black walnut tree which secretes a chemical from its roots that harms plants and vegetation within its vicinity.

Type of symbiosis	Effect of species 1 on species 2	Effect of species 2 on species 1
Mutualism	+	+
Parasitism	+	-
Commensalism	+	0
Amensalism	-	0

Table 7.2: Displaying effects of different types of symbiosis where "+" denotes a positive effect, "-" denotes a negative effect and "0" denotes no effect. Similar tables express this idea, e.g. the one found in Kot [16]

²Rohr defines network architectures as 'combinations of nestedness, mutualistic strength and mutualistic trade off'

Appendices

Appendix A

Chain rule for partial differentiation

Let $f = f(x_1, \dots, x_n)$ and $x_j = g_j(y_1, \dots, y_m)$, $j = 1, \dots, n$, $k = 1, \dots, m$. If f and g are differentiable, then

$$\frac{\partial f}{\partial y_k} = \sum_{j=1}^n \frac{\partial f}{\partial x_j} \frac{\partial x_j}{\partial y_k}.$$

This is the chain rule of partial differentiation [4]

Jacobian Matix

In vector calculus, the Jacobian matrix is the matrix of all first-order partial derivatives of a vector values function. Suppose $F : \mathbb{R}^n \rightarrow \mathbb{R}^m$ is a function given by m real-valued component functions, $F_1(x_1, \dots, x_n), \dots, F_m(x_1, \dots, x_n)$. Should they exist, the partial derivatives of all these functions with respect to the variables can be organised in an $m \times n$ matrix, the Jacobian matrix J of F , as follows

$$J = \begin{pmatrix} \frac{\partial F_1}{\partial x_1} & \frac{\partial F_1}{\partial x_2} & \dots & \frac{\partial F_1}{\partial x_n} \\ \frac{\partial F_2}{\partial x_1} & \frac{\partial F_2}{\partial x_2} & \dots & \frac{\partial F_2}{\partial x_n} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial F_m}{\partial x_1} & \frac{\partial F_m}{\partial x_2} & \dots & \frac{\partial F_m}{\partial x_n} \end{pmatrix},$$

See [13].

Appendix B

MATLAB code used to create figure 6.3

```
h=0.5;
tmax=100;
N1=zeros(1,tmax/h+1);
N2=zeros(1,tmax/h+1);
N1(1)=1;
N2(1)=1;
r1=3;
b1=1;
a12=1;
d1=1;
r2=4;
b2=1;
a21=1;
d2=1;
for k=1:(tmax/h)
N1(k+1)=N1(k)*exp(r1-((b1*N1(k))/(1+a12*N2(k)))-d1*N1(k));
N2(k+1)=N2(k)*exp(r2-((b2*N2(k))/(1+a21*N1(k)))-d2*N2(k))
end
t=0:h:tmax;
```



```
plot(t,N1,t,N2);
```

MATLAB code used to create figure 6.4

```
h=0.01;
tmax=100;
N1=zeros(1,tmax/h+1);
N2=zeros(1,tmax/h+1);
N1(1)=1;
N2(1)=1;
r1=3;
b1=1;
a12=1;
d1=1;
r2=4;
b2=1;
a21=1;
d2=1;
for n=1:(tmax/h)
N1(n+1)=N1(n)+(h*N1(n)*(r1-((b1*N1(n))/(1+a12*N2(n)))-d1*N1(n)));
N2(n+1)=N2(n)+(h*N2(n)*(r2-((b2*N2(n))/(1+a21*N1(n)))-d2*N2(n)));
end
t=0:h:tmax;
plot(t,N1,t,N2);
```

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